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# SELECTION INDEX NUMBERS AND THEIR USE IN BREEDING [1]

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## I. THE NATURE OF THE SELECTION PROCESS

WHATEVER one's views regarding the relative importance of different theories as to the method of inheritance for practical breeding, it must be recognized that the vast majority of all the actual breeding operations which are being carried on by plant and animal breeders at the present time are conducted by some method of selection. The belief is firmly held by most practical breeders that the bulk of the improvement which has been made in domestic plants and animals has been as the result of selection. While it is also coming to be recognized that hybridization may play an extremely important part in breeding operations either by causing increased variation or by bringing about a recombination of characters, according to Mendelian principles, yet selection must always be used as a supplement to hybridizing in practical breeding. The higher degrees of perfection demanded in judging ring and show room are only attained by the most careful and close selection. The manner in which successful selection operates, that is whether by isolation of pure or homozygote strains from a mixed population or by the gradual cumulative effect of adding together slight

[1] Papers from the Biological Laboratory of the Maine Agricultural Experiment Station, Orono, Maine. No. 11.

fluctuating variations, need not here concern us. In either case the breeder is continually meeting the same practical problem of selecting breeding stock with reference to several characters.

It is an obvious fact that a breeder practically never wishes to improve only one single characteristic of the plant or animal which he is breeding. What is usually desired is to improve several characteristics at the same time. Thus, with dairy cattle, while the main object in breeding is to increase the amount and quality of the milk other things such as constitutional vigor, breeding capacity and the like can not be lost sight of in making the selections of breeding stock. Or in maize breeding, to take an illustration from the plant side, while one may be desirous of increasing the protein content of maize, in breeding for it he must always keep in mind the conformation of the ear, size of ear, yield and a whole series of other characteristics.

While it is generally true that one wishes in practical breeding to improve more than one feature at the same time, it is an extremely difficult thing to make concurrently close selection of two or more characteristics of an organism. This difficulty is essentially a psychological one. It is the difficulty of trying to do more than one thing with the mind at the same time. The way in which this operates in breeding by the method of selection may be illustrated by an example. Suppose one is attempting to improve a strain of maize with respect to (*a*) earliness and to (*b*) conformation of the ear at the same time. When beginning his field selection of plants he makes a resolution that he will keep to a certain standard with reference to both of these characteristics and will accept nothing below those standards. Presently he comes to a plant which is by far the earliest in the field. It by a great deal surpasses all others in respect to this character, yet unfortunately the ear of this plant falls below his chosen standard for conformation of ear. What is to be done? Logically the plant ought to be rejected. But

if the breeder is deeply interested in improving the corn with respect to earliness what actually will happen will be this: he will decide to take this plant on account of its earliness and in spite of the defects of the ear. In selection work every degree of compromise of this kind is made and the larger the number of characters one attempts to deal with at the same time the more compromises are made. Where shall the line be drawn beyond which further compromise shall not be permissible?

## II. The Theory of Selection Index Numbers

It would seem to be highly desirable to devise, if possible, some method for the use of the breeder who is practising selection which would get over in a greater or less degree the difficulty which has been outlined in the preceding section. What is needed is some method whereby a selection of several characters may be made at the same time in an absolutely impersonal and impartial manner without throwing out absolutely those individuals which are especially good with respect to a single one of the group of characters undergoing selection and mediocre or poor with respect to the other characters of the group. It has occurred to us that a way of reaching this desired end is found in the use of what we have called "selection index numbers," borrowing the terminology and something of the idea from the literature of political economy.

An "index number" in the sense here used means a single mathematical function which combines in itself the values of several independent or correlated variables. In such a function each of the variables may be weighted in any desired manner to meet the needs of the particular problem. Having decided the relative degree to which each variable shall be weighted, the index number as finally calculated gives an absolutely impartial and impersonal summing up of the total combined value or effect of the variables entering into it.

The theory of a breeding index number may be illus-

trated by a concrete example. Let the matter of improving maize by selective breeding be taken. Suppose that a breeder starts with a promising variety of yellow dent corn. This variety, while promising, has never been improved by breeding at all. The ears are only fair in respect to size and shape. The principal aim of the breeder of this corn, let us suppose, is to increase the "earliness" (*i. e.*, shorten the time of maturing), but at the same time he wishes to improve the other characteristics of the corn—size and shape of ear, relative proportion of corn on cob, and yield per acre. In making field selections of plants to furnish seed for testing out by the "ear-row" or other method, the breeder will endeavor to select with reference to as many as possible of the points enumerated above in addition to "earliness." Further it will be desired after the ears have been harvested and dried to take careful account in selecting the seed of at least the following points: Shape of ear, length of ear, circumference of ear, condition of tip and butt of the ear, kernel shape, germination and proportion of shelled corn to cob. Now if a plant happens to be especially early, even though it be relatively poor in respect to these ear characters, it is likely to be selected to furnish seed, in spite of these defects. But it is possible to devise a formula for a selection index number which shall give whatever weight may be previously agreed upon to each of these several variable characters of the corn which have been enumerated. Having settled upon a particular formula, the selection of seed then becomes essentially a purely mechanical matter so far as the characters included in the formula are concerned. The value of the index will be determined by the relative contributions from each of the included variables. If the breeder calculates such a selection index number, and takes no ears with an index below that standard, it will then be possible for him to select with reference to a series of characters in an unbiased and impartial manner.

Analytically considered a selection index is an expression of the general form

$$I_1 = \phi(x, y, p, q, \cdots, w) \qquad (1)$$

where $I_1$ denotes the selection index and $x$, $y$, $p$, $q$, etc., are the variables upon which it desired to carry out selection. The practical question which has to be solved in forming a selection index in any given case as to what shall be the form of the function $\phi$. The formula for an index should fulfill the following requirements:

1. It should be simple and easily calculated.
2. The value of the index should increase as the desirability of the individual as a breeder increases.
3. The index should be relatively more sensitive to small changes in important characters than to those in unimportant characters; that is, the variables should be differentially weighted.
4. The value of the index should decrease as undesirable characters become relatively marked.

It has seemed to the writers that to a first approximation the following general form of expression will be found to be well suited for a selection index:

$$I_1 = \frac{ax \pm by \pm cz \pm \cdots \pm nw}{a'p \pm b'q \pm c'r \pm \cdots \pm n't} \qquad (2)$$

In this expression $x$, $y$, $z$, $\cdots$, $w$ are variables which become more desirable (*i. e.*, from the breeder's standpoint) as their values *increase;* whereas $p$, $q$, $r$, $\cdots$, $t$ are variables which become more desirable as their values *decrease.*[2] The quantities $a$, $b$, $c$, $\cdots$, $n$, and $a'$, $b'$, $c'$ $\cdots$, $n'$ are constants to be given arbitrary values in the proportions that the different variables are to be weighted.

It will be seen that a selection index number as described above is in a sense an adjunct or supplement to a score card. The index affords a means of condensing the entire information which the score card gives into one unit which can be then dealt with individually.

[2] Cf. actual indices for poultry and corn, pp. 392 and 397 *infra.*

Selection indices of the character above described may be separated into two general categories. These categories may for the sake of convenience be designated as (*a*) fundamental and (*b*) special. A selection index is to be regarded as fundamental when it includes in its formula those characters of an organism which every breeder will wish to maintain at a high grade or improve, whatever may be the special purpose for which he is breeding. Thus, for example, in maize breeding whether the breeder is working for high protein or high oil content or earliness, he will always desire to have well-shaped ears with good tips and of good size, a high yield of shelled corn to the acre and good vitality (*i. e.*, germinative capacity) in his seed.

These and other characteristics which we need not take space here to enumerate are in a sense fundamental or universal characteristics which every breeder wishes to improve or, at least, to keep at a high standard. Similar considerations obtain in breeding dairy cattle or poultry for performance. Besides the performance in respect to milk production or egg production every breeder of these animals desires that what may be called the "breeding capacity" of his stock shall be constantly improved or, at least, not impaired. By "breeding capacity" is meant ability to produce numerous and vigorous healthy offspring, to put the matter in the broadest way. An index number which has to do with these universally desired characters may be called the fundamental selection index for each type of organism.

On the other hand, by a special selection index is to be understood one which includes those characteristics which a breeder is specially and particularly working to improve. In the case of the corn breeder working for high protein, the protein content of the ear will constitute one of his special selection indices either by itself or in combination with some other characters. In dairy cow breeding the butter fat content of the milk will be a special selection index.

What may be called the final selection index may be formed by combining mathematically the fundamental and special indices in a single index number.

## III. A Selection Index for Poultry

The writers are engaged in the experimental breeding of poultry and of maize with reference to utility characters. One of the special aims of the poultry breeding work is to learn how to fix superior egg production in a strain by breeding. In the corn breeding the chief special aim is to improve a strain of sweet corn in respect to earliness, so that it may mature seed under Maine climatic conditions. In connection with this work the idea of selection index numbers has been developed. It is proposed to discuss here the particular selection indices which we are using for poultry and for sweet corn simply as an illustration of the theory of such index numbers and of their application in actual practical breeding operations. It is not our intention to maintain in the least that the indices here given are the best which could be devised or even that they are not subject to change in our own hands with further experience. They are still in the experimental stage. Our only reason for calling attention to the particular forms of indices which we are using at this time is that we believe that the general idea of selection indices as set forth in this paper may prove to be a useful one to the breeder working in other fields. The fundamental idea of a selection index number is a most elastic one. Any one may adopt and modify these indices and weight the different variables, in any way to suit his individual needs. But there is no doubt that a general plan of this kind becomes more intelligible if concrete illustrations of its operation are given. The specific selection indices now to be discussed are presented solely as illustrations of the general theory.

In the case of poultry breeding a fundamentally desirable thing, whatever may be the special object of the

breeder, is reproductive or breeding capacity in the birds. A "200-egg" hen is of very little value *as a breeder* if she is not able to produce when mated with a good male bird a fair precentage of chickens which will live.

It is very generally stated by practical poultrymen that the point on which it is most often decided whether a given commercial venture in the poultry business shall succeed or fail is the expense involved in the hatching and rearing of the chickens. The female that will produce eggs which will yield a high proportion of chickens from the eggs set, and whose chickens live through to marketable age is an extremely desirable bird from a practical standpoint.

The fundamental selection index which we have chosen for poultry relates primarily to the breeding capacity of the female. The value of this index for a particular bird can only be determined after her breeding capacity has been tested. This poultry selection index comes into application in deciding which of the pullets that have been tested as breeders in their pullet year shall be kept over to be used as breeders in their second year of life.

The formula which has been provisionally adopted in our work as a fundamental poultry selection index is as follows:

$$I_1 = \frac{5(a+b)}{c+d+1}$$

The following scheme shows the meaning of the letters in the formula:

$I_1$ = general or fundamental poultry selection index for an individual bird.

$a$ = percentage of this bird's eggs which hatched.

$b$ = percentage of eggs actually laid by this bird to the total number it was possible for her to lay between February 1 and June 1 (*i. e.*, the breeding season) of the year for which the index is calculated.

$c$ = percentage of this bird's eggs which were infertile.

$d$ = percentage of chicks hatched from this bird's eggs

which died within three weeks from the date of hatching.

A brief discussion will make clear the reasons why these particular variables are chosen for the index and are arranged in the formula in the manner that they are. A bird's value as a breeder increases as the percentage of her fertile eggs which hatch increases. Therefore $a$ should go into the numerator of the index fraction. Similarly a bird's value increases as a breeder in proportion to her egg production in the breeding season. A bird which produces few eggs during the breeding season (whatever she may have done before) *ipso facto* can not produce many chickens. Instead of using the actual egg production in the index the relative or percentage production is used, for reasons which have been discussed in a previous publication by the present writers.[3]

Now in distinction to the factors so far discussed it is clear that a hen's value as a breeder decreases as the number of infertile eggs which she produces in a given time increases. To put this factor into the breeding index is, of course, equivalent to asserting that the hen plays at least an equal part with the cock in determining fertility. This is undoubtedly the case, though it is not the place here to present detailed evidence on the point. Since relatively poor fertility of the eggs is an undesirable characteristic $c$ is put in the denominator of the index fraction. The case is the same in regard to $d$. If the chicks produced by a particular bird are weak and die early when given the same treatment as that under which other chicks thrive, it is an indication that that particular bird is not desirable as a breeder.

In order to give a concrete idea of the values which this poultry selection index may take in actual cases Table I has been prepared. This table gives the value of $I_1$ for a number of pullets which were tested as breeders in the spring of 1908, as well as the values of the component factors in each case. The cases given in the table

[3] Cf. Me. Agric. Expt. Station, Bulletin No. 165, pp. 46–48.

are not a random sample of the breeding flock but were definitely selected to illustrate the behavior of the index.

## TABLE I

SHOWING REPRESENTATIVE VALUES OF THE SELECTION INDEX IN POULTRY AND ITS COMPONENT PARTS

DATA FOR BARRED PLYMOUTH ROCK PULLETS[4]

| Band No. of Bird. | A Per Cent. of Fertile Eggs Hatched. | B Percentage Breeding Egg Production. | C Percentage of Eggs Infertile. | D Per Cent. of Chicks Dying within 3 Weeks. | Selection Index $I_1$. | Band No. of Bird. | A Per Cent. of Fertile Eggs Hatched. | B Percentage Breeding Egg Produc ion. | C Percentage of Eggs Infertile. | D Per Cent. of Chicks Dying Within 3 Weeks | Selection ndex $I_1$. |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 10 | 21 | 18.33 | 36 | 33.33 | 2.8 | 29 | 28 | 28.33 | 27 | 0 | 10.0 |
| 160 | 9 | 15.83 | 42 | 0 | 2.9 | 23 | 39 | 35.83 | 28 | 8.33 | 10.0 |
| 402 | 14 | 33.33 | 30 | 50.00 | 2.9 | 428 | 46 | 40.08 | 20 | 22.22 | 10.0 |
| 352 | 12 | 41.67 | 14 | 60.00 | 3.6 | 122 | 49 | 34.17 | 15 | 23.53 | 10.5 |
| 358 | 50 | 31.67 | 32 | 69.23 | 4.0 | 375 | 41 | 37.50 | 36 | 0 | 10.6 |
| 438 | 35 | 35.00 | 45 | 37 50 | 4.2 | 712 | 42 | 50.00 | 20 | 20.00 | 11.2 |
| 441 | 38 | 20.00 | 33 | 33.33 | 4.3 | 408 | 48 | 45.86 | 16 | 22.73 | 11.8 |
| 21 | 25 | 35.00 | 14 | 44.44 | 5.0 | 38 | 61 | 37.50 | 9 | 28.00 | 13.0 |
| 393 | 12 | 47.50 | 9 | 50.00 | 5.0 | 731 | 27 | 35.83 | 23 | 0 | 13.1 |
| 705 | 38 | 26.67 | 34 | 25.00 | 5.4 | 395 | 29 | 37.50 | 24 | 0 | 13.3 |
| 717 | 24 | 21.67 | 19 | 20.00 | 5.7 | 443 | 56 | 54.17 | 6 | 35.29 | 13.3 |
| 39 | 23 | 29.17 | 26 | 16.67 | 6.0 | 409 | 37 | 46.67 | 4 | 25.00 | 13.9 |
| 377 | 32 | 37.50 | 16 | 33.33 | 6.9 | 771 | 43 | 60.00 | 13 | 22.22 | 14.2 |
| 746 | 59 | 28.33 | 15 | 47.06 | 6.9 | 19 | 68 | 24.17 | 24 | 6.66 | 14.5 |
| 87 | 36 | 39.17 | 17 | 35.71 | 7.0 | 152 | 26 | 39.17 | 11 | 9.09 | 15.5 |
| 359 | 61 | 32.50 | 15 | 50.00 | 7.1 | 366 | 52 | 25.83 | 13 | 7.14 | 18.4 |
| 442 | 41 | 68.33 | 38 | 28.57 | 8.2 | 768 | 74 | 45.00 | 20 | 9.38 | 19.6 |
| 400 | 44 | 47.50 | 16 | 38.10 | 8.2 | 434 | 72 | 58.33 | 17 | 14.28 | 20.2 |
| 27 | 18 | 40.00 | 8.3 | 25.00 | 8.5 | 750 | 57 | 52.50 | 16 | 10.00 | 20.3 |
| 757 | 23 | 51.67 | 10 | 30.77 | 8.9 | 770 | 71 | 50.83 | 9.8 | 12.82 | 25.8 |
| 725 | 33 | 29.17 | 6 | 27.27 | 9.1 | 752 | 48 | 59.17 | 6 | 12.50 | 27.5 |
| 112 | 17 | 46.67 | 18 | 25.00 | 9.3 | 397 | 38 | 40.00 | 6 | 5.89 | 30.3 |
| 753 | 61 | 47.50 | 46 | 10.53 | 9.4 | 168 | 88 | 35.83 | 4.7 | 13.89 | 31.6 |
| 407 | 41 | 41.67 | 18 | 23 53 | 9.7 | 749 | 57 | 46.50 | 4 | 6.45 | 45.2 |

From this table the following points are to be noted:

1. The selection index ranges in value between 2.8 and 45.2 in the cases chosen for illustration. These figures do not represent the extreme values which may be obtained for this index. They suffice, however, to bring out the point of practical importance that the index fluctuates through a wide numerical range as the value of the birds as breeders changes.

[4] It should be said that all the records given in this table were made under uniform conditions as to housing, feed, age of birds, etc. The hatching was all done in incubators.

2. A study of the detailed figures of the table makes it apparent that the index is a perfectly impartial and accurate measure of a bird's breeding performance. Thus to take an example, bird no. 402 has a low selection index (2.9), while bird no. 168 has an index more than ten times larger (31.6). Do these figures represent fairly the difference between these two birds in respect to breeding performance? Let us examine the detailed figures. But 14 per cent. of the fertile eggs from bird no. 402 hatched as against 88 per cent. of the fertile eggs of no. 168. In regard to number of eggs laid during the breeding season the two birds are about equal, with what advantage there is in favor of no. 168. But on turning to the question of fertility of eggs we see that 30 per cent. of the eggs of no. 402 were infertile as against only 4.7 per cent. in the case of no. 168. The same condition obtains in regard to the vitality of the chicks. Fifty per cent. of the chicks from no. 402 died before attaining the age of three weeks, whereas but 13.89 per cent. of no. 168's chicks died within this time. There is no doubt of the great superiority of 168 over 402 in breeding performance. The index gives an exact measure of its degree or amount.

3. The detailed figures bring out clearly the further point that the value taken by the index is not unduly influenced by any one factor. Low values for one variable may be offset by high ones in another. In general, the variables which form the numerator of the index fraction are seen to increase as the index increases. The reverse holds in general for the variables in the denominator of the index. The facts regarding the two variables, $a$ (percentage of fertile eggs hatched) and $c$ (percentage of infertile eggs) are shown graphically in Fig. 1.

The diagram shows that the percentage of fertile eggs hatched in general increases as the selection index increases in value, but with much greater fluctuations from bird to bird. On the other hand the percentage of infertile eggs in general decreases as the value of the index increases, but again with much greater fluctuations. The

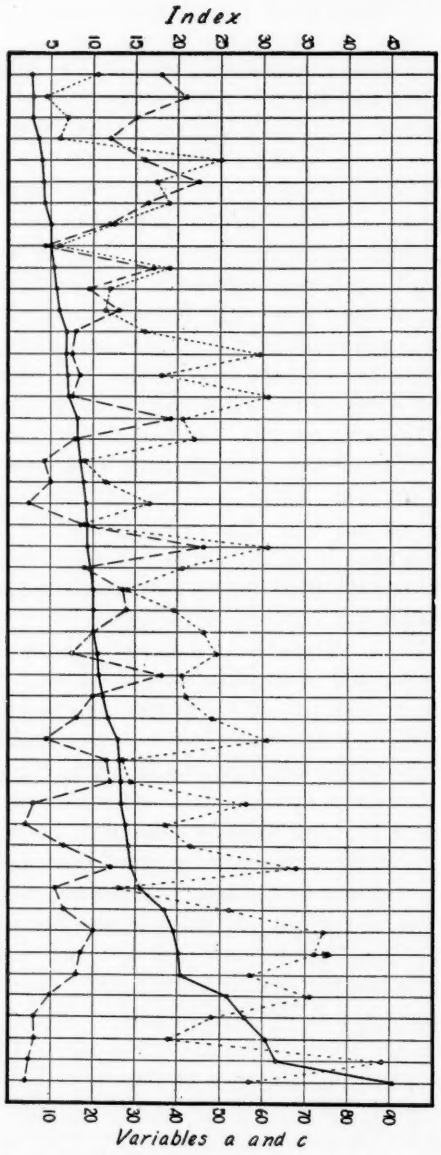


FIG. 1. Diagram showing the relation to the value of the selection index of the order given in Table I; O———O selection index; o.....o percentage of two of the variables entering into it. The abscissæ denote the birds arranged in fertile eggs hatched; ●---● percentage of infertile eggs.

smoothing effect of combining the four variables into one index number appears most clearly from the diagram.

4. In Table I, one half of the birds have a selection index equal to or greater than 10. This is about the value which it would seem desirable to take as a division point in selecting breeders. A bird with an index below 10 can not be regarded as a good breeder.

Summarizing, we believe the poultry selection index described, or some modification of it to suit particular needs, to be a useful aid in practical breeding operations with poultry. It measures in an exact and impartial manner the performance of a bird as a breeder in any given season. On the basis of the knowledge so gained the breeder can select birds which are to be retained for further breeding. It substitutes an exact and impartial measure, in the place of a rough, general impression of the relative effect of several variables.

## IV. A Selection Index for Sweet Corn

The idea of selection index numbers is being applied in connection with investigations in breeding sweet corn (*Zea Mays saccharata*). In this work the selection index is based on the characters of the ear. A brief discussion of this index is introduced here for two reasons, viz., (*a*) to illustrate the adaptability of the selection index idea to widely different classes of breeding problems, and (*b*) to show how such index numbers supplement the score card in breeding operations. In planning this corn selection index the underlying idea was that set forth by way of example earlier in the paper (p. 386, *supra*).

The actual index number used for sweet corn has the following formula:

$$I_1 = \frac{A + 3B + 2C}{D + E + F^2}$$

The meaning of the letters in the equation are shown in the following scheme.

$A$ = Length of ear multiplied by the circumference of the ear ($L \times$ Cir.). This gives a measure of the absolute size of the ear.

$$B = \frac{\text{100 times the weight of grains shelled from butt and tip of ear.}}{\text{Total weight of shelled corn from whole ear}}$$

$B$ is the percentage which the grain on butt and tip is of total grain on the ear. This gives a measure of the extent to which ends of the ear are covered with grain.

$$C = \frac{\text{100 times the circumference of the cob at the middle of the ear.}}{\text{Circumference of ear at middle.}}$$

This measures in effect the average percentage depth of kernel (by difference).

$$D = \frac{\text{100 times the weight of the cob.}}{\text{Total weight of shelled corn from the whole ear.}}$$

$E$ = (circumference of ear at butt) − (circumference of ear at tip). A measure of the shape of the ear.

$F$ = 100 − the observed percentage germination of grain from this ear.

All measurements and determinations are made on the thoroughly dried ear and are recorded in centimeters and grams.

As an illustration of the way in which this index is calculated a single example may be worked out in detail.

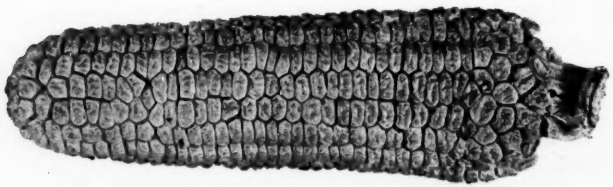

FIG. 2. Photograph of sweet corn ear No. 596 for which the selection index number is calculated in the text.

Let us determine the value of $I_1$ for the ear of sweet corn shown in Fig. 2, and recorded in our notes as ear No. 596.

For this ear the following measurements were recorded:

| | |
|---|---|
| Length | 14.8 cm. |
| Circumference | 12.9 " |
| Weight | 118.0 gr. |
| Weight of shelled corn | 97.0 " |
| Weight of corn shelled from butt and tip | 22.8 " |
| Weight of cob | 21.0 " |
| Cob circumference | 7.9 cm. |
| Butt circumference | 9.3 " |
| Tip circumference | 6.5 " |
| Rows | 16 |
| Number of kernels in average row | 33 |
| Germination (100 kernels tested) | 100 per cent. |

Using these data to calculate the selection index it appears that:

$$A = 14.8 \times 12.9 = 190.9$$

$$B = \frac{100 \times 22.8}{97.0} = 23.5$$

$$3B = 70.5$$

$$C = \frac{100 \times 7.9}{12.9} = 61.2$$

$$2C = 122.4$$

$$D = \frac{100 \times 21.0}{97.0} = 21.6$$

$$E = 9.3 - 6.5 = 2.8$$

$$F = 100 - 100 = 0$$

$$F^2 = 0$$

Whence we have:

$$I_1 = \frac{190.0 + 70.5 + 122.4}{21.6 + 2.8 + 0} = \frac{333.8}{24.4} = 15.7$$

The value of the index in this case is much above the average for the particular variety of sweet corn of which this ear is a representative. This is, of course, as it should be, since the ear is a particularly fine one for sweet corn. Its aristocratic lineage is apparent from the photograph. Some ears of this variety give a value for the index of as low as 1.0 or even lower. It is obvious that the index number for an ear of one variety is not directly comparable with that for an ear from another

variety. Corn index numbers, as formulated above, are only directly comparable within a single variety. They may of course just as well be used in judging a dent corn, for example, as for the sweet corn here discussed. The average ear of dent corn will obviously give a different value for the index from that given by the average ear of sweet corn.

Any one familiar with the score cards used in judging corn in the various agricultural shows and fairs in this country will recognize that the corn selection index formula here given combines in one expression quantitative determinations of a majority of the characters which appear on the score card. The index in a way takes the place of the judge. It impartially "cuts for each defect" according to a previously agreed upon system of weights. By the combined use of the index number, scales and measuring tape, unconscious or conscious partiality and bias is inevitably and absolutely taken out of the judging. The selection index idea seems capable, when properly developed to meet the needs of particular cases, of supplying in some measure that thing which has been so long desired in all kinds of stock judging, whether of plants or animals, viz., an *absolute* base or datum plane.

## V. SUMMARY

The purpose of this paper is to call the attention of those interested in breeding operations to the usefulness of what we have called "selection index numbers" in such work. The idea of such index numbers is to combine in a single numerical expression the values of a series of variable characters with regard to all of which the breeder wishes to practise selection at the same time. The analytical expression of this idea is discussed and its adaptability and usefulness are illustrated by examples drawn from poultry and maize breeding. It is shown that selection index numbers form a valuable adjunct to the score card in stock judging.

# A CONTRIBUTION TO THE THEORY OF ORTHOGENESIS [1]

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SEVERAL reasons have been given why biological discussion has, for a number of years, ceased to center about the fact of evolution and is now chiefly concerned with the factors, for such is evidently the case: the principal aim of modern biological researches is apparently to throw light upon the question of method. It is now a part of common knowledge that Darwin considered the natural selection of fluctuating variations to be the principal factor in evolution, and some of his successors have gone so far as to see in it a sufficient one; but, while few biologists will probably be disposed to deny that natural selection is an efficient factor in evolution, there seems to be now on hand a sufficient body of data to show that it is far from being the only one. Among other methods[2] that have been emphasized, mutation and orthogenesis may be mentioned, each of which has its adherents, and it is the last named of these that seems to be the principal one concerned in the evolution of a group of snakes that I have recently monographed—the genus *Thamnophis* (the garter-snakes).[3]

I will briefly summarize the conditions that prevail in this group:

1. The genus *Thamnophis* consists of four groups of

[1] Read at the Darwinian Celebration of the Michigan Academy of Science, April 1, 1909.

[2] I mention only these three (selection, mutation and orthogenesis), as they appear to me to be the only ones that can be considered to have been dominant methods in the evolution of the forms in the genus that constitutes the basis of this discussion.

[3] Ruthven, Alexander G., "Variations and Genetic Relationships of the Garter-snakes," Bull. 61, U. S. Nat. Museum.

closely related forms, each group ranging both northward and southward from the Mexican plateau (which is their center of dispersal) into North and Middle America.

2. Each group consists of a series of forms, the ranges of which adjoin and correspond to different geographical regions.

3. The forms of the same group may intergrade or not, but in either case they come in contact where the geographic conditions with which they are associated meet, and the areas of transition in characters correspond to the areas of intermediate environmental conditions. When the forms intergrade the transition in characters takes place gradually in the intermediate region, and where there is apparently no intergrading at present the two forms become most like each other in this region, there being no abrupt changes in characters between two directly related forms.

4. Each group tends to become progressively more dwarfed away from the Mexican plateau, each form usually being more dwarfed than its neighbor toward the center of origin, and less so than the representative whose range adjoins it on the side away from the center.

5. The relative size is correlated with the number of labials and rows of body scales, and these two characters —size and scutellation—constitute the only apparent specific differences, except in the few cases where they are accompanied by differences in color or relative tail-length.

6. The amount of dwarfing is not associated with particular geographic regions, but the scutellation and relative size of any form is that of its immediate ancestor plus the dwarfing which it has itself undergone. Thus a dwarf form of one group frequently occurs in the same region with a much less dwarfed representative of another group, the difference in relative size being due to differences in the number of forms between the one in question and the center of origin.

7. The variations in the characters of each form fluctu-

ate about a mean, and the transition in characters between the different forms is brought about by a gradual variation of the average type.

Students of evolution problems will recognize in this summary (*a*) the old story of the association of different forms with different environmental conditions, (*b*) the so-called definite or determinate evolution, and (*c*) that the phylogenetic variations are gradual.

It has long been noted that, among animals of the same group, the different forms are generally associated with different environmental conditions. In some cases it seems that these forms may occupy different habitats in the same environment, but in by far the greater number of instances, at least among terrestrial animals, directly related forms inhabit different, but neighboring, geographic areas. That there is some connection between the differentiation of such a group and the diversities of the region it occupies has usually been assumed; at least it is a fact that must be considered in any explanation of evolution. It is explained by natural selection on the assumption that the different conditions in the two regions demand different adaptations on the part of the organism, but this explanation will apparently not hold in the case of the garter-snakes, for there is certainly no advantage in dwarfing *per se*. It might be assumed (and it would be pure assumption) that this trait is correlated with unperceived adaptative characters, but this would seemingly be trying harder to save the theory of natural selection than to explain the facts. I have pointed out that there is no relation between the amount of dwarfing and particular habitats, but that forms (belonging to different groups) of quite diverse scutellation may occupy the same region. Apparently the conditions in each region do not call for a particular size (as would, it seems to me, be *approximately* the case if the struggle for existence in each habitat required that the forms become dwarfed), but only act to modify to some extent the invading form, the relative size of the latter being

determined as much by the modifications which the group has previously undergone as by those to which the particular form has been subjected.

I believe that these objections to the operation of selection in the evolution of these forms also argue against De Vries's mutation theory as an explanation, for, while it is easily conceived that mutations may have arisen within the limits of fluctuating variation in each case, we must also assume that the new form pushed into the new environment, or at least now occupies it to the exclusion of immediately related forms, because better fitted for it, which does not seem to be the case. What seems to have actually taken place is that as each group pushed out from the center of origin it became modified each time it encountered a new region of environmental conditions, not by the selection of forms better adapted to the new conditions, but by the modification of the entire section that invaded the new region. This may be tested more thoroughly by an examination of the method of evolution.

Perhaps the most striking characteristic of this genus is the manner in which evolution has taken place along definite lines. Although the forms frequently have other distinctive characters, they nearly all have this in common that they are more dwarfed than the form from which they have been derived, and there is no case in the genus where a form is larger than its neighbor toward the center of origin. The history of each group has thus been one of progressive dwarfing as it departed from the center of dispersal.

It is too often overlooked by students of evolution that natural selection can cause directed evolution (orthoselection); for in order that it may do so it is only necessary that there be an accruing advantage in the increased development of a character. The characters must thus be utilitarian, however, which is apparently not true in this case. Moreover, it would certainly be taxing the theory to make it account for the continued development

in the same direction in the four groups, when one considers the great variety of conditions with which they are associated. To explain this definite development on the basis of orthoselection it would be necessary to adopt the point of view that each form in each group found it of advantage in the struggle for existence in its particular environment to become more dwarfed than its immediate ancestor, which is to my mind unthinkable when one considers that we have in this genus four groups that push out in all directions from the center of origin, into desert, grassland and forest regions, in the tropical and temperate zones, and yet in every case the modifications associated with each region are practically of the same nature and non-adaptive. We meet the same difficulties if we attempt to apply the mutation theory to explain this definite evolution, for, while de Vries's mutants arise suddenly and are definite steps in new directions, he states in regard to the accumulation of characters:[4]

> It is not by mere chance that the variations move in the required direction. They do go, according to Darwin's view, in all directions, or at least in many. If these include the useful ones, and if this is repeated a number of times, cumulation is possible; if not, there is simply no progression, and its type remains stable through the ages.

It seems from this that in order to explain the evolution of a group by a series of modifications more or less similar in kind the mutation theory of de Vries is forced to fall back upon natural selection. If I have rightly interpreted the conditions, I believe that natural selection, with or without the assistance of the mutation theory, fails as an explanation of the definite evolution of this genus, and that we have here an example of true orthogenesis, *i. e.*, progressive modifications in each group without the aid of natural selection.

The nature of the variations is very interesting in several ways, and throws further light on the problem, for, although one must be cautious of forming conclu-

[4] De Vries, H., "Species and Varieties, Their Origin by Mutation," p. 572.

sions on this subject without the controlling evidence of experimentation, certain general relations seem to be apparent.

I have stated that the variations in each form fluctuate about a mean, but that this mean varies, approaching in the intermediate region that which characterizes the next form on its line of descent. That the different forms also originated in this way is shown in the numerous instances where they actually intergrade. This is essentially the idea of mutation (in the sense of Waagen and Scott) or "phylogenetic variation", which is not to be distinguished from individual variation by any character of quality or quantity, but by the fact that it pursues a determinate direction by the gradual shifting of the normal type. Conn[5] states that:

> It should be noticed that these considerations in regard to variations along definite lines have less significance in connection with such characters as can be supposed to advance by general averages. Some organs have been advancing in definite directions for long generations, but if the advance consists of an increase or decrease in size of the organs there is not needed any law of determinate variation to explain the matter. If it be an advantage to have an organ increase in size, and if variations in this organ occur around an average type, then without any necessity of supposing a special law directing variations, we can understand how natural selection will continue to increase the size of the organ in question.

All this is very true, for it is only orthoselection working on the average type, but as selection seems to be debarred in this case, the characters being non-utilitarian, we apparently have in the garter-snakes a case of evolution along fixed lines as the result of definite variation. Even if we could admit the selection of fluctuating variations as the dominant factor in the evolution of these forms, we should encounter the additional difficulty that it (selection) is apparently unable to create a new species, the form slipping back to the original condition when the selection ceases. The nature of the variations also seems to me to debar de Vries's theory of mutations as a

[5] Conn, H. W., "The Method of Evolution," p. 146.

possible explanation, for, according to de Vries, the specific changes are sudden and fixed, the new race appearing fully formed, which is certainly not the case in these snakes, unless we consider the new race as having been formed by small successive mutations of the same kind, which would, if I understand him rightly, be contrary to de Vries's idea of mutations, for he says that they "take place so far as experience goes without definite direction." We have apparently in these snakes an example of definite but gradual variation, in that there is in each group a gradual development of forms along a fixed path, without the aid of natural selection.

A theory that accounts for the definite evolution of this genus without the aid of selection is that there has been in each group a gradual modification of the forms under the influence of the environment. The determinate variation of the average type, the close association of the forms with different geographic regions and the consequent correspondence of areas of transition in characters with intermediate geographical conditions, would seem to render this conclusion unavoidable, if, as seems evident, selection is not operative here. It should be noted, however, that, while the evolution of the genus has been distinctly orthogenetic and associated with the environment, it does not appear that the latter has, as has often been supposed by adherents of this theory, a specific effect. This would be difficult to determine if we were dealing with one group, for example one that pushed northward from the Mexican plateau, for here there would be an increasing difference in climatic conditions, associated with accumulated modifications, between the range occupied by the form at the center and that of the most outlying species. But when all four groups are considered it is seen that the same modifications appear whether the group is pushing into the tropic or temperate regions, or into deserts, semi-arid plains, or humid forests, and it is difficult to conceive of environmental conditions common to all of the regions occupied

by these snakes that would exert such a specific effect upon them. It seems rather that throughout the genus the germ cells have such a restricted number of potential responses that the different groups have tended to vary in the same direction (homoplasy) under the influence of the environments which have been encountered; that is to say, the similarity of the response is conditioned by the constitution of the animal, the environment only acting as a stimulus upon the germ cells.

This theory would seem to satisfactorily explain why some directly related forms intergrade while others do not, for if infertility is in proportion to physiological diversity, as Darwin held, it is quite evident that as the new form produced as a group pushes into a new region becomes more or less modified, it will also probably become physiologically different from the parent stock and be more or less unable to cross back. This is essentially Eimer's Genepistasis, or Entwicklungstillstand, the standing still of certain forms at definite stages in development while others continue. But it should be noted in this case that the forms that progress each time are always associated with new geographic regions, and do not occur, as Eimer holds that they can, in the same region with the parent stock.

In conclusion I would like to point out that the purpose of this paper is to describe the method of evolution in the genus *Thamnophis* rather than to discuss the cause of the variations. It is evident that the suggested relation between the action of the environment and the nature of the response of the organism can only be tested by experimentation. I may add further that the interpretation offered of the conditions in this genus depends upon whether or not the relationships of the forms and the lines of development are as outlined. In pursuing work of this kind it soon becomes apparent that the relationships of any form can only be determined with certainty when the conditions that prevail throughout the genus have been examined carefully, and, conversely, that erroneous

ideas of relationships are very liable to result from incomplete knowledge of the course of evolution in the group, so that it is very hazardous to select a few forms of a genus and endeavor to discover the laws governing their development. An illustration can be drawn from this genus: *butleri,* which lies entirely within the range of *sirtalis,* may, so far as its characters go, easily be conceived to have been derived from the latter, and, if so, a different theory of the factors involved in its evolution must be sought to explain its origin. That it has more probably been developed from *radix* by dwarfing only becomes relatively certain when the lines of evolution in the genus have been worked out. This should discourage attempts to adduce as evidence for or against any theory the relationships of particular forms before the genus has been studied as a whole, and the general lines of development determined.

# THE "PRESENCE AND ABSENCE" HYPOTHESIS[1]

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IN Mendel's[2] discussion of the behavior of characteristics in the offspring of splitting hybrids, the phenomena of segregation are described in terms of pairs of antagonistic characters. He assumed that these are represented by pairs of internal units, one member of each such pair coming from one parent, the other from the other parent. This idea of pairs of characters in Mendelian hybrids has been generally entertained until somewhat recently, and is still perhaps not uncommonly held. De Vries[3] made use of this conception in stating what he thought to be a fundamental distinction between species and varieties, assuming that the differentiating features of varieties are represented by units which are homologous with corresponding units of the species from which such varieties sprang, and which are paired with those units on crossing, while different species lack such homology and pairing of determiners.

About six years ago in a paper on Mirabilis crosses, Correns[4] stated the members of several Mendelian "pairs of characters," as the presence and absence of *single* characters. Cuénot[5] in a paper doubtless written simul-

[1] Read before the Botanical Society of America, at Baltimore, December 31, 1908.

[2] Mendel, J. G. "Versuche über Pflanzen-Hybriden." *Verhandlung des Naturforscher-Vereines.* Brünn IV. 47 pp., 1866.

[3] De Vries, H. "Species and Varieties: Their Origin by Mutation," pp. 847, 1904. See p. 251 *et seq.*

[4] Correns, C. "Weitere Beiträge zur Kenntnis der dominierenden Merkmale und der Mosaikbildung der Bastarde." *Ber. d. deutsch. Bot. Ges.* **21**: 195–201, Ap. 23, 1903.

[5] Cuénot, L. "L'hérédité de la pigmentation chez les souris" (2me note). *Arch. de Zool. éxpér. et gén.*, **1** (4th S.): 33–41, 1903.

taneously with Correns's paper, but published several months later, used the same expression,[6] and most recent writers on Mendelian inheritance have adopted the method of presenting the characters in the terms of presence and absence.[7]

But while this change of usage has gradually taken place, little attention has been given to the real significance of the newer method of statement, except by Hurst,[8] who gives a good general discussion of the presence and absence hypothesis in a paper read before the Third International Conference of Genetics two years ago.

Hurst showed that of 44 Mendelian characteristics of various plants and animals studied by him, 41, or more than 93 per cent., can be appropriately described in terms of presence and absence. As one reviews these various characteristics, he can not avoid the feeling that in a number of cases the presence and absence could be read quite as well backward as forward, and it will doubtless be impossible in many cases to decide which is the positive character and which its absence. Thus in the contrast between a yellow and a green pea, the yellow is described

[6] Cuénot has not followed up the idea however in the development of a consistent usage, but continues to treat the supposedly antagonistic characters as if they are alike positive and represented by antagonistic internal units which he conceives to be the chromosomes. The idea that the chromosomes are the determiners of the Mendelian unit-characters has been also advocated by Spillman, but the latter appears to accept the correctness of the presence and absence hypothesis.

[7] Davenport considers "presence and absence" a relatively rare phenomenon. He says: "I think it is clear that dominance in heredity appears when a stronger determiner meets a weaker determiner in the germ. The extreme case is that in which the strong determiner meets a determiner so weak as to be practically absent as when a red flower is crossed with a white." (Davenport, C. B. "Determination of Dominance in Mendelian Inheritance." *Proc. Amer. Phil. Soc.*, 47: 59–63, 1908. See p. 63.) In papers which have come to hand since my paper was read at Baltimore, Bateson and his co-workers, and Castle have, on the other hand, declared unequivocally for the presence and absence hypothesis, as having general validity. See Bateson, Saunders and Punnett, "Experimental Studies in the Physiology of Heredity." Reports to the Evolution Committee of the Royal Society, IV, pp. 40, 1908, see p. 2, and Castle, W. E., "A Mendelian View of Sex-heredity," *Science*, N. S., 29: 395–400, March 5, 1909.

[8] Hurst, C. C. "Mendelian Characters in Plants and Animals." Report of the Third International Conference on Genetics, pp. 114–128, 1906.

as present in the yellow pea and absent in the green pea. What is to hinder us from describing the green as present in the green pea and absent in the yellow one? Similarly in the contrast between tall and dwarf, one could perhaps say "presence and absence of dwarfness on a tall basis" as appropriately as "presence and absence of tallness on a dwarf basis," and there seems no sufficient reason why the palm type of leaf in Primula should not just as well be considered a shortened fern type, as the fern an elongated palm type, or that the thrum is a shortened pin-eye quite as well as that the pin-eye is an elongated thrum. But notwithstanding such difficulties as these, there can be no question that most of the phenomena of Mendelian inheritance are more simply stated in terms of presence and absence than in any other way.

It has appeared to several writers as a difficulty for this hypothesis that in a number of cases what appears to be the absence of a character is dominant over its presence. There are a number of noteworthy cases of this kind. Thus, in cattle the hornless condition is dominant over horns; in most breeds of poultry white plumage dominates over colors and white legs over yellow legs; in snails unbanded shells dominate over banded, and less banded over more banded; in wheat, smooth heads dominate over bearded; in flowers having a yellow plastid color, white is dominant over yellow; in canary birds the presence of a mottled pattern is dominated by its absence, though in most cases color patterns are dominant over their absence. Thus in the mottled varieties of beans, for instance, the mottling factor is dominant over its absence, and in rabbits, the English-marked, Dutch-marked, tan-marked, tortoise-yellow, and agouti patterns are in each case dominant over their absence.

At several places Hurst states (*loc. cit.*) that the assumption that a certain character is the presence-character would "imply the dominance of that character," though in eight instances among the 44 he cites, he definitely places the absence dominant over presence. In

speaking of thrum and pin-eye Primulas (p. 122) he says:

> If we regard it as presence and absence of pin on a thrum basis this would imply dominance of pin over thrum in the zygote.

Again regarding the dominance of short hair over Angora in rabbits (p. 125) he says:

> If on the other hand we regard it as presence and absence of Angora on a short basis, this would imply dominance of Angora over short in the zygote.

Both Bateson and Davenport appear to have tacitly agreed that the dominance of absence over presence is a difficulty for the "presence and absence" hypothesis, for both have taken occasion to explain that what appears to be the absence of a character may really be the presence of a positive inhibiting factor. Indeed, Davenport[9] has taken the position that the positiveness of a character determines its dominance, and, therefore, all cases in which the absence of an external character dominates its presence must be explained by the existence of a positive factor in whose presence the given external character can not be produced. Thus, he says:

> A progressive variation, one which means a further stage in ontogeny . . . will be dominant; a variation that is due to abbreviation of the ontogenetic process, which depends on something having dropped out, will be recessive.

While I recognize the probability that there are positive inhibiting factors, as well as factors which produce specific structural and color characters, I think it can be shown that such an assumption is not necessary for the explanation of the dominance of the absence of a character over its presence. I will assume for the sake of the discussion that the presence and absence hypothesis is correct, and that the absence is real, having no internal unit to represent it. This assumption seems to me, as it did to Hurst, to be simpler and more practical than the alternative idea that the internal units are paired in the heterozygote, having a representative for absence as well as one for presence. I believe there is no fact on record[10]

[9] Davenport, C. B. Report of the Third International Conference on Genetics, p. 139, 1906.

[10] Except perhaps so-called "spurious allelomorphism."

which can not be as well explained on the basis of a single unit, as a pair of units.

On this basis the fundamental difference between the three classes of individuals produced by self-fertilization of a heterozygote may be simply stated thus: There are two classes of homozygotes, usually designated *DD* and *RR*, and the heterozygote, usually referred to as *DR*. The difference between the two kinds of homozygotes with respect to any unit-character is, that one—usually the *DD*—has one pair of allelomorphs or "genes"[11] in addition to those possessed by the other kind of homozygote—usually the *RR*. As the two kinds of homozygotes are often not appropriately called dominant and recessive, I will call the one which has the added pair of genes (*i. e.*, the one which has $2n+2$ genes) the "positive" homozygote, and the one which lacks them (*i. e.*, the one with only $2n$ genes) the "negative" homozygote. If we designate collectively the common features of two parents which differ from each other in a single unit-character by the letters *BB*, and the differentiating genes by the letter *A* repeated as often as the gene is repeated in each nucleus of the soma or sporophyte, the positive homozygote will have the composition *AABB*, the negative homozygote will be simply *BB*, and the heterozygote will be *ABB;* and whatever differences are observable in these three classes of individuals must be due obviously to the presence of none, one, or two "*A*" genes in each nucleus and to the reactions of these with the underlying factors which have been here collectively represented by "*BB*."

In order to see the bearing of these assumptions upon questions of dominance we must consider briefly the nature of the unit-characters. Regarding the nature of the genes themselves—the primary character-producing

[11] This word is proposed by Dr. Johannsen as a substitute for words such as pangenes, ids, allelomorphs, etc., which have been used to denote an internal something or condition upon whose presence an elementary morphological or physiological characteristic depends. The word "gene" has the advantage that it does not assume by its form or derivation any hypothesis as to the ultimate character, origin or behavior of the determining factor.

units—I have nothing to suggest, for to that question I am, like Professor Bateson,[12] inclined "to hold my fancy on a tight rein;" but there can be no doubt that the *visible* Mendelian characters are always secondary, and but little doubt that they are all dependent at some stage of analysis upon chemical relations.

This is too obvious to need discussion in the case of color-characters, and in those structural characters which involve only some by-product of the metabolism of the cells as, for instance, the starchy or sugary character of the endosperm in maize. It requires perhaps a more daring flight at present to assert that such structural characters as hairiness, branching, lobation and serration of leaves, production of horns, extra toes, different forms of comb, etc., which involve the number, direction and succession of cell-divisions, depend likewise upon the intimate chemical nature of the protoplasts; but even if it could be shown that *physical* properties of the protoplasm are to a certain degree determining conditions of cell-division, the resulting structures could hardly conceivably be permanent hereditary features, unless these physical properties are dependent at last upon the chemical composition of the protoplasm.

Having arrived at the conclusion that all the Mendelian characters are dependent upon chemical relations, we may return to the question of dominance, and the relation between the two kinds of homozygotes and the heterozygote, and see to what extent the known facts may be interpreted in terms of chemical experience.

A fundamental principle in this connection is the law that the extent of a reaction between two chemicals is determined by the amount of that reagent which is present in less relative quantity, and not by the one which is present in excess. When the positive homozygote, *AABB*, and the heterozygote, *ABB*, are alike, *i. e.*, when there is complete dominance of presence over absence, it

[12] Bateson, W. The Methods and Scope of Genetics, 49 pp., Cambridge, The University Press, 1908. See p. 12.

may mean that already the presence of the one unit *A* of the heterozygote is sufficient to result in the maximum reaction, in which case the doubled factor *AA* of the positive homozygote can do no more. When, on the other hand, one unit *A* is not sufficient to produce a maximum reaction with the other factors present, the *AA* of the homozygote produces the corresponding character in greater intensity, and the heterozygote will be intermediate between the two homozygous parents. Both of these conditions are frequently realized.

The case I have wished to deal with specifically is that in which the heterozygote—the *ABB* individual—does not differ in external aspect from the *negative* homozygote, *BB*, so that the ratio becomes 1:3 instead of 3:1, this is the situation in which the absence of a character is dominant over its presence. In such a case the character determined by *A* is latent in the heterozygote. To show that this situation is possible it need only be pointed out that in a number of familiar instances a precipitate is formed or some other visible reaction takes place only in the presence of a certain excess of one of the reagents. It is perfectly clear that in any such case, one may add nearly enough of the reagent which is required to be in excess, and no apparent reaction will take place, but if the quantity of this reagent be doubled the characteristic reaction will occur. Now this is just what I conceive may take place in certain crosses. In the heterozygote where the chemical unit *A* (of whatever nature) occurs but once in each nucleus, no reaction becomes apparent, but in the pure-bred forms bearing the unit *A* in double quantity, *i. e.*, *AA*, the specific character (or reaction) produced by this unit appears. The heterozygotes will then be indistinguishable from the negative homozygote, and in the offspring of two heterozygotes bred together there will be among every four individuals on the average three which have the character absent and one which has it present, or in other words "absence will be dominant over presence."

Very neat laboratory experiments can be arranged to illustrate this behavior, with any reaction in which a certain excess of one of the reagents is required, and while these reactions will probably be in most cases of much greater simplicity than those presented by the interaction of the hereditary units, and they can, therefore, be considered only as presenting analogies, I am convinced that such analogies are not unfair ones.

It is especially easy to arrange an experiment showing such a result in the case of certain organic substances known as indicators, as litmus and phenolphthalein, for here one needs to assume only that the single, unpaired unit in the heterozygote produces such a quantity of acid or alkali as will not quite change the character of the cell-sap of the negative homozygote with respect to acidity or alkalinity. Thus if I make an alkaline solution of litmus and add to it as the product of one assumed unit, *A*, such a quantity of any acid as leaves the solution still slightly alkaline, I may allow this to represent the heterozygote. Then the homozygote possessing the acid-producing unit *A* will have it in double quantity or intensity. When I add this second portion of acid to the solution it is instantly changed from alkaline to acid, as is indicated by a change from blue to red color. The negative homozygote lacking the acid-producing unit and the two heterozygotes are alike blue, while the individual which is pure with respect to this unit whose specific external manifestation is the production of a red color, alone possesses that character, and this results in a realization of the ratio, 3 absences to 1 presence, or the dominance of absence over presence. This example has the advantage of being conceivably duplicated in the case of many vegetable color-characters, for the very widely distributed anthocyan which gives the red and blue colors is an indicator similar to litmus, and could have been used in this experiment instead of litmus.

Whether the situation here outlined is actually attained in the case of red and blue flowers in nature can not per-

haps be demonstrated. It is the general experience that blueness is dominant over its absence, but this is just the result I have pictured here as a case in which absence of redness or of acidity is dominant over its presence. I know of no way of determining whether red flowers are blue flowers with an added factor for acidity, or whether blue flowers are red with an added factor for alkalinity, and, indeed, it is conceivable that both of these situations may be presented in different species. However, my purpose is attained if I have shown that there is no greater theoretical difficulty involved in the dominance of absence over presence than in the dominance of presence over absence, and that the assumption that any given character is due to the presence of an added internal unit does not "imply the dominance" of that character.

The non-appearance of an externally visible character in the heterozygote, although the corresponding internal unit is present, as must always be the case when real absence is dominant over presence, plainly presents a kind of latency somewhat different from the four types recognized by me[13] in a recent article in the AMERICAN NATURALIST. For the sake of uniformity with the terminology there adopted I may call this new kind of invisibility "*latency due to heterozygosis.*" Like all the other types of latency except that due to fluctuation, the latency resulting from heterozygosis produces no deviation from definite characteristic ratios.

I recall at present only one case in which we can certainly identify latency due to heterozygosis, for the reason that, just as we have seen above in regard to blue and red flowers, it may be quite impossible in any particular instance to decide which is the positive character and which its absence. In a particularly interesting cross between a yellow and a reddish snail, Lang[14] has found

[13] Shull, G. H. "A New Mendelian Ratio and Several Types of Latency," AMERICAN NATURALIST, 42: 433–451, July, 1908.

[14] Lang, A. Ueber die Bastarde von Helix hortensis Müller und Helix nemoralis L. Eine Untersuchung zur experimentellen Vererbungslehre. Jena: G. Fischer. 1908.

that the heterozygotes are yellow when young and red when they grow older. In this case the appearance of yellow in the young stage leaves no doubt that this is the fundamental color upon which the red is superposed. The pure bred red snail—the positive homozygote—is red from its earliest stages. This latency of the red character in the young heterozygotes produces a dominance of the absence of red over its presence in the early stages of development, and if the snails are classified at this time, the $F_2$ is found to consist of 3 yellows to 1 red. Later in life the heterozygotes become red and the census shows 3 reds to 1 yellow.

The rather frequent occurrence of heterozygotes lacking the usually dominant character may be quite appropriately said to present cases of latency due to the combination of fluctuation and heterozygosis.

## Summary

The "presence and absence" hypothesis assumes that what appears to be a pair of characters in Mendelian inheritance is really the presence and absence of a single character. This hypothesis has now won the support of most of the leading experimental students of heredity. The fact that the absence of certain characters dominates over their presence has appeared to some to be a difficulty. This paper shows that no such difficulty is involved and simple chemical experiments are cited which, if duplicated among plants and animals, as they no doubt are, would give the dominance of absence over presence, without recourse to "inhibiting factors."

When absence dominates over presence the positive character is latent in the heterozygote. Such cases may be said to show *latency due to heterozygosis*. This condition is exemplified by some of Lang's snail crosses. The same phenomenon is involved in many cases of failure of dominance in heterozygotes.

Station for Experimental Evolution,
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# PRESENT PROBLEMS IN PLANT ECOLOGY[1]

## III. Vegetation and Altitude

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In the study of the relation of plants to environment, there are few problems of greater interest than those presented by the vegetation of mountains. The general facts are somewhat familiar, and reference to them is here necessarily brief. Whatever the vegetation of the surrounding country, mountains are usually forested; the forest is often composed of several zones in which different kinds of trees successively predominate; higher up the forests finally cease and give place to grassland of perennial herbs and low shrubs—these are some of the more general facts of mountain vegetation. There is bound up with them not only strangeness and beauty, but also a series of most interesting problems in the ecology of plants.

If I understand rightly the reason for this symposium, my duty is to state, as well as in brief compass I may, the present state of our knowledge in regard to these phenomena. In general, they rest back upon physical environment. In so saying, however, it must be kept in mind that biotic factors early modify the primitive physical ones; the reason for the occurrence or absence of a species may be the conditions created by other species.

The important factors which vary with altitude seem to be heat, light, precipitation, evaporation, and a factor made up of several of those named, namely, length of season. Let us consider these severally, and try how far

[1] A series of papers presented before the Botanical Society of America, at the Baltimore meeting, by invitation of the council.

we may at present determine the part played by each in connection with the plant life of mountains.

1. *Heat.*—From the days of Humboldt to the present, the vast importance of temperature in this connection has been recognized. In spite of this, our knowledge is rather scanty and vague. It has been usual to attribute great importance to the severe cold of mountain tops. This view, however, is entirely open to challenge. Mountains which rise up from warm plains certainly can not be invaded by plants which are killed by frost, but is there warrant in any physiological knowledge we now possess for supposing that extreme low temperatures are of any especial significance for plants which endure freezing? There is reason for believing that some woody plants are cracked by severe cold, but I believe the general question must be answered in the negative. That treeless mountain tops are not so because of great cold is shown by two facts: First, in cases that have been investigated, timber lines do not bear any direct relation to isothermal lines; and furthermore, forests do exist in the coldest districts on the globe. Herbaceous plants, too, taken even in the active condition, are known to survive extremely low temperatures, undisturbed.

We may note in passing the obvious fact that, for most low growing mountain plants, deeply buried as they are under snow, extreme winter temperatures do not come in for consideration at all.

That the lower temperatures of air and soil during the growing season are factors of great importance is not to be doubted. More specific information is not easy to obtain. Direct observation avails nothing, for we can hardly point to a single feature of anatomy or histology which is called forth by or conditioned upon heat or cold. In order to make further progress, recourse is naturally had to instrumental study. In the use of this method, many pitfalls await the worker. It is relatively easy to secure data of temperature, but *vastly difficult to interpret them.* It seems to me that, seeing a good

many ecologists are making use of temperature data, this point will bear some emphasis. Feeling that ecology is new, and exact instrumental work is the kind that counts, it is very easy, when one has secured a fine series of readings, or better still, a complete thermographic tracing for a growing season, to entertain the impression that he has accomplished something of note; whereas the fact in the matter simply is that if he has done his work well, it is of a quality with the routine work of a weather bureau. To relate the physical data to the manifold activities of a living plant is another matter, and calls for all the power of critical thought and all the knowledge of physiology which any man can command.

For our purpose, it seems possible to do little more than to point out some difficulties to be surmounted. To begin with, any method which assigns increasing values to higher temperatures must go astray as soon as the plant's optimum is passed, and for most of the plants we are dealing with, we do not know where that is. If, also, as there is some reason to believe, the growth-temperature curve has more than one maximum, a still further difficulty would be brought in.

Furthermore the ecologic optimum is made up of many harmonic optima, and may vary in different life phases of the same plant. In experiments in forcing fruit trees, it has been found that the optimum for blooming is markedly lower than for other periods for the plant's activity. Finally the temperatures recorded are for the soil or air, whereas the ones wanted are those that prevail within the plant. Leaves and shoots are warmed by sunshine and cooled by the evaporation of water. In this way temperatures may be brought about which differ materially from those recorded by a thermometer alongside. In the case of an Alpine plant, sheltered in some sunny angle of rock, how widely the temperature within its leaves may differ from that shown by a thermometer near by, properly set up for air temperatures in shade!

On the positive side, there seems less to be said. It

can not be doubted that the plant life of mountains is in no small degree modified and controlled by temperature, but who can put his finger on definite facts and say "this temperate forest is on this mountain in the tropics because of temperature," or "this Alpine plant is a dwarf because of cold." Strongly as we may suspect such points, we must be cautious about including them within the realm of our positive knowledge.

The peculiarities of Alpine plants have been thought to be due, in part, to great daily variation in temperature; that owing to the greater clearness and rarity of the atmosphere, the plant is more exposed to heating by intense sunshine by day, and cooling by more rapid radiation at night. Since growth takes place particularly at night, it seems evident that marked night cooling would lead to reduced size. That this is actually true has been proven by placing growing plants each night in the ice chest. At present more light is chiefly needed as to what temperatures are really experienced by Alpine plants over night. Air temperatures, at any rate, are more equable at high altitudes. In connection with the work in the Selkirks during the past summer, two complete thermographic records were taken, one meter from the surface, same hillside and exposure, at altitudes of 800 m. and 1,700 m., respectively. The daily maxima recorded at the upper station were notably less than at the lower; the nightly minima only slightly so. (Freezing point was not recorded for many weeks.) Such data accord well with the general results of meteorologists. They refer of course only to air temperatures.

Briefly summarizing, we may say that our knowledge of the relation of heat to mountain vegetation is not great. The importance of extreme low temperatures has been much overestimated. The significance of moderate temperatures is not yet capable of exact interpretation. The hypothesis of night cooling as a cause of alpine dwarfing needs further physical facts as a basis.

2. *Precipitation.*—That mountains are islands of

greater precipitation and that the vegetation of mountains is largely dependent upon atmospheric water are ideas familiar to every one. Schimper has further suggested that light showers at high altitudes favor the development of grassland rather than forest. This idea, to be tenable, requires the further assumption that the soil in the grassland zone is deficient in water supply. This may be true for lower latitudes, but it scarcely seems admissible for northern mountains where the late melting snows leave the soil supplied with all the water it can hold.

In quite a different way, too, precipitation in the form of snow becomes a decisive factor for vegetation. In a paper read before this society, a year ago, I showed that the timber line of the Selkirks was due to the heavy snow beds at those altitudes. By a coincidence, Cowles showed elsewhere, at the same time, that in a number of places in North America snow beds and timber line were causally related.

3. Closely connected with the question of heat and precipitation is another factor of prime importance in some mountains, namely, *Length of Season.*

In respect to this factor at least two points of view are necessary. For trees and plants growing on wind-swept spots, length of season is a question of temperature. For the vast majority of low-growing plants, on the other hand, length of season is also a question of emergence from snow beds to air and sunshine.

Taking up, first, the question of forests, it has been said that the total heat available at high altitudes is not sufficient for the maturing of new wood, and more particularly, that the season is too short for the ripening of good seed. Both of these ideas must stand or fall simply upon evidence, and so far as I am aware, none of a reliable character has been brought forward. It may be remarked that seedling trees usually seem abundant enough at timber line. It would be of interest to gather seeds of balsams, etc., growing at timber line and learn

if they germinated properly. When one considers the fact that elevated forests are usually coniferous, Myake's studies on photosynthesis by evergreen trees during winter become of interest. One may well inquire if trees of this kind obtain in this way a distinct advantage over others at high altitudes.

Turning to the low growing plants, we find their problems of a somewhat different nature. In the Alps, the Caucasus, the northern Rockies and the Selkirks to mention only a few examples, large tracts of lofty grassland lie buried under snow until the close of the vernal period. If one visits the higher forests of the Selkirks in June, he must journey in the snow. Arriving at the alpine fields, he finds them at the summer solstice, still hidden under an almost unbroken covering of white. In the month that follows, they will be gradually exposed. During the ten or fifteen weeks that remain, they must accomplish nearly the whole sum of their annual activities. The ability to do this must be a decisive factor in their struggle for existence. *Carex nigricans* ordinarily occurs mingled with other plants; but in moist hollows, where the snow has lingered until the middle of July, it often forms patches to the entire exclusion of competitors. Where the snow does not melt till the first of August, it is absent and the visible vegetation consists of polytrichum only. Where snow persists till late in August, the soil thus exposed is destitute of visible vegetation. Walking in the verdant alpine fields at the end of August, one finds each unmelted patch of snow bordered by plant societies in the order mentioned. Do we not read in this that of phanerogamous plants present the sedge is best able to compress its life processes into a brief period; that the moss is able to live with even shorter time allowance, but that even the moss is unable to maintain itself under conditions of such brevity of season as are represented by twenty or thirty days at the close of summer? It is hardly to be doubted that many other less easily traced questions of association and occurrence are decided by length of season.

4. *Light.*—Since a certain proportion of light is absorbed during passage through the atmosphere and particularly by the layers next the earth's surface, it seems plain that light becomes more intense with increasing altitude. If so, its relation to vegetation is a matter of much interest.

Notwithstanding that the question has received considerable attention, our knowledge of it is still in a rather unsatisfactory condition as will appear from the following:

Bonnier, Schimper, Schroeter and indeed most of those who have written upon the subject, express the belief that the more intense light is a factor of importance in connection with Alpine vegetation. They give reasons indicating that a greater intensity exists, and noting the reduced leaves and shoots and prominent flowers of alpine plants, state that the former is the cause—in part at least—of the latter. The conclusion, however, has not been put to the test of discriminating experiment.

Any further discussion of the subject brings in a general consideration of light as an ecological factor. I trust a brief digression may be permissible.

Since light is a form of solar energy, efforts have naturally been made to compute its intensity from astronomical data. Attempts have been made in several quarters to calculate light intensity for any day and hour of sunshine for the year at a given latitude. They do not, however, seem to have been happy in escaping fundamental error. For, in making calculations from the sun's altitude, there is not one varying factor, but several which must be reckoned with: (1) The amount of radiant energy falling upon a horizontal surface varies with the sine of the sun's altitude. This law is perceived by every one. It has sometimes been neglected, in the thought apparently, that since leaves stand at all angles, it is unnecessary to reckon what a horizontal surface may receive. Yet the direct light available for the total vegetation of a hectare or any other area is func-

tioned upon the angle made with the sun's rays. The law of the sine may, therefore, not be neglected. (2) Within the atmosphere we have the phenomenon of diffuse light from the sky. At the earth's surface it becomes a factor of no small importance, very likely surpassing for vegetation in general that of the direct rays of the sun. It is, of course, derived from direct light, but for it the law of the sine is far from valid. In general, it is subject to less variation. It is probably affected by many factors not easily observed, presence of dust, vapor, etc., and its numerical computation borders on the impossible. A table showing light intensity for any given day or hour, might possibly, if all factors were taken into account, show the value of direct light, but it is open to question, if this is what the botanist chiefly wants to know. (3) The length of the path of a ray of light through the earth's atmosphere, and, therefore, the fraction of it which is absorbed, increases with decreasing elevation of the sun. Quite apart from diminution due to decreasing angle of incidence, the light wanes as the sun approaches the horizon. This fact is sometimes clearly seen; sometimes apparently overlooked. (4) Absorption in the lower, denser, dust, water-vapor and carbon dioxide bearing layers of the atmosphere is relatively far greater than in the upper and rarer ones. This last holds good, especially for the shorter rays. This third consideration comes to the foreground in a study of altitude and vegetation.

Here then are several varying factors; some of them difficult to calculate, and none of which may be neglected. Moreover, as will be shown below, there is reason for doubting whether any theoretical calculations are valid, even for clear days.

Wiesner has carried on extensive studies upon light and plants, extending over several decades. He offers data to prove that light, for a given time and place, with cloudless sky, can by no means be calculated from astronomical data. His readings taken in different parts of

the world show astonishing irregularities. In Buitenzorg, the light diminished rapidly between eleven and twelve o'clock under apparently clear sky. Similar data were recorded for Cairo, Egypt. The maximum intensity obtained anywhere in the world was not in the tropics, but in Yellowstone Park. Though some of his results seem rather incredible, it must be owned that his methods appear ample and critical—far beyond anything else undertaken by a botanist. He has emphasized the distinction between direct and diffuse light. He finds the proportion of the former to increase greatly with altitude, and sees in this a factor of much importance for vegetation. His results in regards to altitude and light are not so full as could be wished, but he attributes the maximum observed in the Yellowstone to altitude, and, in general, assigns a high importance to light as a factor in alpine climate.

On the other hand, Clements states that in Colorado the variation of light with altitude amounts to a very small percentage and concludes that such differences as exist are too small to receive serious consideration in a study of mountain vegetation. The chief thing, therefore, that appears certain is that the whole question is in an unsatisfactory condition. In such a situation, one or two points must be kept clearly in view.

First, data as to light intensity must be obtained by methods which will pass muster with physicists. A certain body of such data are available. Time is lacking to take up the question here, but the work of Cayley, Violle, Langley and others might be cited to show that a considerable increase in light intensity with altitude does exist.

In the second place, it must be borne in mind that the relation of the plant to light is a complex one. In some of the work above quoted there seems to be the wholesale error of assuming that the importance of light for the plant is to be judged by observation upon its relation to the process of photosynthesis. It seems super-

fluous to emphasize that light is not only a source of energy, but a factor which now stimulates, now inhibits various activities of the plant in a profound degree.

It is the highly refrangible rays which suffer greatest absorption by the atmosphere. The light at the surface would, therefore, differ in *quality* from that at higher altitudes. In studying the question, it appeared to me desirable to learn whether any responses by plants could be found to alterations in quality—alterations, nevertheless, in which all kinds of rays should still be present. I therefore endeavored to set up experiments which should merely add a proportion of certain rays to an already sufficient daylight illumination. The results, while far from being as full and conclusive as could be wished, seem to indicate pretty clearly that plants do respond to such a variation in quality. Internodes were observably shorter and leaves more hairy under the bluer light.

Perhaps the whole question can be summed up in saying that the relation of vegetation to variations in light due to altitude are poorly understood; that more data from trained physicists would be welcome, but that the experiments still remain to be made which would enable us to interpret such data with confidence.

5. *Evaporation.*—Since pressure becomes less, wind velocity increases, and insolation becomes greater with increasing altitude, it has seemed necessary to conclude that the evaporation rate increases. Toward the summits of many mountains, *e. g.,* the White Mountains and Adirondacks, the decisive relation of wind to forest vegetation can hardly be doubted. In these cases there is good ground for assigning evaporation as the cause of timber line with all that it involves. The death of buds and twigs is probably chiefly due to drying in cold weather.

Most of the leading writers agree without question that evaporation is more rapid at higher altitudes. Schimper lays much emphasis upon it; Schroeter writes vividly of the drying of skin experienced by alpinists

and mentions the dry cured meat prepared by peasants in some places in the Alps, which, it is stated, is due to the greater drying power of the air. The reasoning is all but conclusive. There can be no doubt though, that the verdict of the soundest reasoning ought to be confirmed in the court of experimental evidence.

In 1907, Livingstone measured evaporation in the Santo Catalina mountains and found a *decrease* with altitude. This, perhaps, was not surprising, seeing that the series began in the desert below and extended to the cool mountain regions above.

During the past summer, I set up two series of instruments in the Selkirks at altitudes ranging from 800 m. to 2,900 m. Mountain flanks having a fairly uniform exposure were chosen, only short horizontal distances were involved, two stations were chosen at each altitude so that one might check the other. The season was favorable, being unusually warm and dry; one series was in perfect operation for twelve weeks. The results on the whole seem to exclude the idea that in the Selkirks evaporation increases with altitude. The maximum in each case was at the next lowest station, altitude of 1,100 meters. Above that there was a gradual and irregular diminution. It may be that the lower temperatures of higher altitudes more than offset the factors which make for increased evaporation. Indeed, it appears certain from the above data that for the Selkirks, such is the case.

The data in question, however, present only weekly totals. The possibility that excessive evaporation may take place during certain portions of the day, still remains to be studied. It must be ever kept in view, too, that it is not the absolute amount of transpiration which is so much of importance to the plant, as the balance between water supply and water loss. If the lower soil temperatures of higher altitudes make the obtaining of water more difficult, then the same or even a diminished evaporation rate might demand increased power of resistance on the part of the plant.

In trying to unravel the problems of mountain vegetation, it must never be forgotten that the plants of the present are descended from preexisting ones; facts of heredity are everywhere; phenomena that are found today not seldom hark back to conditions of the past.

In concluding, allow me to offer a plea for a service, which I have been thinking for several years would be one of the most helpful which could be rendered to this adolescent science of ecology, namely, that some one whose knowledge of physics and physiology fits him for such a task should overhaul and scrutinize our ideas and methods. Not counting minor and ephemeral papers, there can be no question that ecology, at the present time, contains not a little of discernible error. Rumors have been heard that zoologists are beginning to study ecology and looking to botanical methods for hints for developing their own. Within the family, it may be said that if wide-awake guests are coming, it is time to set the house in order. Moreover, ecology is finding a large place in elementary text-books, and in this way errors are being propagated. The interest alike of science and education in this field could in no way be better served than by a relentless pruning.

DISCUSSION OF PROFESSOR SHAW'S PAPER.

DR. LIVINGSTON: A remark was made by Professor Shaw in the beginning of his paper, which suggests that we sometimes lose sight of physical facts. A certain plant is not killed or shut out by the fact that other plants are near it, but by the fact that light conditions or moisture conditions or evaporation conditions or temperature conditions are different from those in which they might live. It seems to me that to speak of biotic and physical conditions leads to confusion; the thing the plant feels must be a physical thing.

PROFESSOR SHAW: In my remark I meant to clear up certain cases where one might lose sight of the fact that plants had largely modified physical conditions. I presume the very case which gave rise to that sentence was this: there are some reasons for supposing that in the Selkirks, the zone of greatest moistness, where lichens and mosses flourish is at something like 4,000 feet in altitude. A forest has developed there, and the condition of low evaporation rate has come about on account of that forest.

# SHORTER ARTICLES AND CORRESPONDENCE

## PLEISTOCENE SWAMP DEPOSITS IN VIRGINIA

Buried swamp deposits of Pleistocene age are far more abundant in the Atlantic coastal plain than was suspected a few years ago. A large number of such deposits are exposed by the comparatively recent cutting of the waves along the western shores of the Chesapeake Bay and the estuaries of our southern rivers. These deposits vary greatly in botanical interest from point to point. In some no recognizable remains have been found, in others these are limited to the stumps of the cypress, while still others contain the remains of a considerable flora. It seems evident that quite a number of modern species are more restricted in their northward range than they were during certain interglacial periods or even post-glacial time, while others are extending their range at the present time. Among the former the red bud or Judas-tree (*Cercis canadensis* Linné) and the osage orange (*Tokylon pomiferum* Raf.) might be mentioned, both occurring in the interglacial beds of the Don Valley near Toronto in Canada. Another species abundant as far northward as New Jersey in inter- or post-glacial time was the bald cypress (*Taxodium distichum* Rich.), and the loblolly pine (*Pinus taeda* Linné) also appears to have withdrawn southward since the late Pleistocene. The water elm (*Planera aquatica* Gmel.), on the other hand, appears to have retreated southward in the late Pleistocene and to be readvancing at the present time.

Numerous Pleistocene swamp deposits are described in the recently published account of the Maryland Pleistocene[1] and their contained fossil plants have been admirably exploited by Dr. Hollick, who enumerates over 40 species from beds of this age in Maryland.[2] Similar deposits are to be found at many points in the Old Dominion, although very little attention has been thus far devoted to their description.

In 1906 the writer described[3] *Fagus americana* (nuts) Vitis sp. (seeds), *Hicoria glabra* (fruit), *Taxodium distichum* (seeds

[1] Maryland Geol. Surv., Pliocene and Pleist., 1906.

[2] *Ibid.*, Systematic Paleont., pp. 217–237, pl. 67–75.

[3] Berry, *Torreya*, Vol. 6, pp. 88–90, 1906.

and cone-scales) and *Nyssa biflora* (seeds) from the Talbot or latest Pleistocene formation at Tappahannock, Va.

During the last two years peat deposits of late Pleistocene age have been discovered at numerous points along the Potomac, Rappahannock and James rivers. These usually contain characteristic stumps of the cypress, often of large size, and the associated peat furnishes recognizable plant remains, generally seeds, of Nyssa, Vitis, Fagus and Taxodium, the latter usually the most abundant. Associated with the plant remains are fragments of the elytra of beetles, occasional insect galls and molluscan remains. Evidently most of these Pleistocene peats indicate the presence of cypress swamps, but this is not always the case, since in some instances we find representatives of upland vegetation, while in other cases the fossils show that the vegetation was open and marsh-like with a scattering of trees of oak, birch and pine. Where quiet water conditions followed the subsiding forest-bed, deposits of clay are to be found and these often contain fragments of leaves along with casts of the shells of Unio if the locality is toward the head of the ancient estuary, or shells of *Rangia cuneata* if the waters were more saline. The latter is very abundant in Pleistocene deposits of this sort from Maryland southward and it is also a member of the modern fauna, confined, however, in the latter case to the Gulf of Mexico.

Fig. 1 shows the bed of massive hard peat a short distance above Tappahannock, Va., from which the above mentioned species were collected. It is exposed for a thickness of four or five feet and shows many cypress stumps in place with the "knees" protruding through the recent narrow sand-beach. Overlying the peat is a layer of drab plastic clay from one to four feet thick and carrying fragments of leaves. Above this there is from ten to fifteen feet of coarse sand. The Rappahannock has cut into the bluff along its south bank, exposing this old cypress swamp for a distance of over one half a mile.

Where the forest-bed was succeeded by waters which were agitated by wave action or swift currents the overlying deposits are sands or gravels laid down on the more or less planed surface of the old swamp. Fig. 2 shows such a condition of affairs in an exposure just above the junction of Parrotts Creek with the Rappahannock River. The line of apparent unconformity is sharply defined running across the center of the picture. Below are seen the cypress trunks and roots embedded in an impure peat which was planed off by wave or current action as the

FIG. 1. Talbot Cypress—Swamp near Tappahannock, Virginia.

FIG. 2. Talbot swamp deposit just above junction of Parrotts Creek and the Rappahannock River.

swamp subsided. Upon this surface lie the coarse sands shown in the upper half of the photograph.

The additions to the Pleistocene flora of Virginia are enumerated below. Those from below Port Royal were collected by Dr. L. W. Stephenson, of the U. S. Geological Survey, who has also kindly furnished the two photographs here reproduced.

FAGALES

BETULA NIGRA Linné.

Knowlton, *Amer. Geol.*, vol. 18, p. 371, 1896.
Berry, *Journ. Geol.*, vol. 15, p. 341, 1907.
———, AMER. NAT., vol. 41, p. 692, pl. 2, figs. 2–4, 1907.

This riverside and flood-plane species appears to be abundant in the swamp deposits of our southern coastal plain, due doubtless to its abundance along the rivers which contributed their flotage to these deposits. The present occurrence is based upon leaves from the right bank of the Rappahannock River one and one half miles below Port Royal.

QUERCUS sp.

A number of fragments of leaves, evidently those of some oak but too fragmentary for even tentative specific determination, are contained in the collection from the right bank of the Rappahannock River one and one half miles below Port Royal, and undeterminable acorns occur in the Talbot deposits near the Nomini Cliffs on the south shore of the Potomac.

FAGUS AMERICANA Sweet.

Hollick, Md. Geol. Surv., Pli. and Pleist., p. 226, 1906.
Berry, *Torreya*, vol. 6, p. 88, 1906.
———, *Journ. Geol.*, vol. 15, p. 341, 1907.
———, AMER. NAT., vol. 41, p. 692, pl. 2, fig. 7, 1907.
*Fagus ferruginea* Michx., Lesq., *Am. Journ. Sci.*, vol. 27, p. 363, 1859.
———, Geol. Tenn., p. 427, pl. 7 (K), fig. 11, 1869.
*Fagus ferruginea* Ait., Knowlton, *Amer. Geol.*, vol. 18, p. 371, 1896.
Mercer, *Journ. Phila. Acad.* (11), vol. 11, pp. 277, 281, fig. 8 (15), 1899.

The characteristic leaves and burrs of this species occur in the Talbot deposits near the Nomini Cliffs. No nuts were found associated with the other remains, but an extended search was not made. This species was one of the commonest trees of the Pleistocene if we may judge from its abundant remains at a large number of localities in Pennsylvania, Maryland, Virginia, West Virginia, Tennessee, North Carolina and Alabama.

CELTIS OCCIDENTALIS Linné.

Bony endocarps, or stones, sometimes enclosed in the lignitized

exocarp, and not distinguishable from those of the modern tree, occur in the peat deposits near Tappahannock. In the modern flora this wide-spread species ranges from the Atlantic to the Pacific and from southern Canada to eastern Texas and Florida. It has not heretofore been recorded in the fossil state. The genus dates back to the middle Eocene in this country, but it is not abundantly represented at any horizons. Leaves described as *Celtis pseudo-crassifolia* by Hollick[4] occur in the older Pleistocene (Sunderland) of Maryland. Abroad the genus is commonly represented in the late Tertiary, at least two species being recorded from the Pliocene, but none so far as the writer is aware from the Pleistocene.

SPINDALES

ILEX CASSINE Linné.

This species which in the modern flora is a denizen of low woods and river banks near the coast from Virginia to Florida and west to Louisiana has not heretofore been found fossil. Eight specimens of leaves are in the collection from the right bank of the Rappahannock River one and one half miles below Port Royal. They are identical with the less elongated leaves of the modern plant and would seem to indicate, if their habitat has remained unchanged, that the Talbot coast line was much farther to the west of where it is to-day, a fact fully borne out by the areal distribution of the deposits of the Talbot Sea. They also show that in Talbot time this species ranged somewhat farther north than it does at the present time, since southern Virginia marks its present northern limit according to Sudworth.

ERICALES

DENDRIUM PLEISTOCENICUM Berry.

Berry, *Journ. Geol.*, vol. 15, p. 346, 1907.

Leaves of this species described originally from the Pleistocene of central North Carolina are present from one and one half miles below Port Royal on the Rappahannock River. They are considerably smaller than the North Carolina leaves, but are identical with them in outline and venation and they are also very similar to the leaves of the existing *Dendrium buxifolium* (Berg.) Desv. As previously pointed out, they probably represent the ancestral form from which the modern upland species, *Dendrium hugeri* and the pine-barren species *Dendrium buxifolium* were derived.

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[4] Hollick, *loc. cit.*, p. 230, pl. 71, fig. 9.

# NOTES AND LITERATURE

## HEREDITY

**A Case of Non-Mendelian Heredity.**—That hereditary characters which behave in accordance with Mendel's law of segregation depend in some way upon the chromosomes can hardly be questioned. Biologists, however, have been loath to believe that all hereditary characters are thus related to chromosomes. It is especially gratifying, therefore, to find completely worked out a type of inheritance which differs radically from the Mendelian type and which appears to be entirely cytoplasmic in character. The law of transmission in this case is of unusual interest. The case is reported by Dr. Erwin Baur, of Berlin.[1]

In this paper Dr. Baur describes several types of variegation. The first consists of variegation due to pathological conditions (auto-infection or auto-intoxication) and is not hereditary. By overcoming the auto-intoxication such plants are converted into ordinary green plants. On the other hand, ordinary plants can be infected with this condition by graft-symbiosis with an infected plant. This condition is not transmitted by seed. It is called by the author "infectious chlorosis," and is accompanied by a partial loss of green pigment in the chlorophyll grains. Several previous papers on this type of chlorosis by the author are referred to.

The second type of variegation consists of fully constant races whose chromatophores carry a diminished amount of green coloring matter, but the normal amount of yellow coloring matter. These races have distinctly yellowish-green leaves. In crosses with green races the yellowish green behaves as a Mendelian recessive.

The readers of this journal will remember that a similar character in tomatoes was reported recently by Professors Price and Drinkard, of the Virginia Experiment Station, and the character in this case behaved also as a Mendelian recessive.

[1] Erwin Baur. The Nature and Hereditary Relations of the Albo-Marginate Horticultural Variety of *Pelargonium zonale*. *Zeitsch. f. Abst.- u. Vererb.*, Bd. I, 1909, H. 4.

In another class of yellowish-green races, which are in a sense constant, the yellow-green plants are all heterozygote and Mendelize into one fourth clear yellow incapable of development, one fourth pure green, constant in later generations, and two fourths yellow-green, which splits again as above. This case was treated of by Dr. Baur in a former paper.[2]

Many other types of variegation exist. One of them is reported in the review of Professor Correns's paper below. The present paper of Dr. Baur's deals with another type of variegation, namely: white margined leaves, such as those found in varieties of *Acer negundo, Cornus alba, Pelargonium zonale* and numerous other species. The investigation was confined largely to the last-mentioned species. Little was previously known of the inheritance of this character. Several authorities had stated that such plants (with white margined leaves) produce only seedlings that are pure white and incapable of development.

Dr. Baur's studies show that the white margined plants of *P. zonale* are covered with two or three layers of cells containing colorless chromatophores which can not assimilate $CO_2$ but which can manufacture starch from sugar. The whole plant is covered by this white tissue. Near the leaf margin the two white layers form the whole of the tissue and thus give the peculiar marking on these leaves.

The line of demarcation between the white cells and ordinary cells is definite. One gets the impression that all the descendants of a white cell are white and all those of a green cell are green. This can not be definitely determined by microscopic study, but the experimental results reported below practically prove that such is the case.

Four white margined plants obtained from different sources all, when self-fertilized, produced only white seedlings, which soon died because they were incapable of assimilating $CO_2$. Some of these plants occasionally produced green branches which arose by the green tissue breaking through the superficial covering of white. Seed from these green branches produced normal green plants which propagated true to seed. On the other hand, white branches, when close fertilized, produced only white seedlings. (An occasional branch was pure white without the underlying green tissue.)

[2] *Ber. d. Den. Bot. Gesell.*, 25, 1907, p. 442, and *Zeitsch. f. Abst.- u. Ver.*, 1, 1908, p. 124.

Crosses made between flowers on pure white branches and other flowers on ordinary green plants gave thirty-nine green seedlings and seven green-white marbled plants. These crosses were made both ways, but only one seed, resulting in a green plant, was raised from the cross of green (♂) on white (♀).

Several crosses made both ways between white margined plants and ordinary green plants gave 199 pure green, 41 green-white marbled, and 4 pure white seedlings. Crosses between white margined and pure white branches gave all pure white seedlings. Evidently, white branches and white margined branches produce only white gametes, while green branches or green plants produce only green gametes.

Of the green-white marbled seedlings—that is, green and white spotted, some formed only white leaves and died when the spotted cotyledons ceased to function.

A second class formed only green leaves and became ordinary green plants when the spotted cotyledons dropped off. Their seedlings, about 50 in number, were all ordinary green plants.

A third class grew stems that were white on some sides and green on others. On such stems leaves attached to white surface were wholly white, and those attached to green surface were wholly green. Leaves attached on the line of union between green and white were correspondingly green and white. Branches which grew from the axils of the leaves behaved in exactly the same way as the leaves in regard to the green and white color.

These facts render it clear that the marbled seedling consists of two kinds of tissue—green and white. The descendants of white cells are white and those of green cells are green. A green and white seedling or branch may become either green or white by the growing point becoming overcapped by the one or the other kind of tissue. Of 23 marbled plants observed 20 became green and two white in this manner.

But the development of a marbled branch or plant may proceed in a different manner and one which clears up the difficulty concerning the nature and hereditary relations of the white marbled plants. In a marbled stem the line of contact between the two kinds of tissue may extend radially inward, or the white tissue may extend in a thin layer some distance over the green. A leaf rising centrally on a line of contact extending radially inward will be half white and half green; but a bud originating

from a part of the stem where the green tissue is covered by a thin layer of white is itself constituted of green tissue covered by white and produces ordinary white margined leaves. New albomarginate plants may thus be obtained from these marbled seedlings by taking branches which thus arise from parts of the stem where the white tissue forms a thin layer over the green. The white margined plants are thus to be regarded as "periclinal chimeras," while the marbled plants are "sectorial chimeras." White or green branches may arise from the white margined plants as the result of irregularity in cell division at the growing point.

The inheritance of the albomarginate character is now clear. In a white margined plant pollen and ovules are produced from white tissue only and hence carry only the white character. The seedlings are therefore white.

Sectorial chimeras were found in which the green tissue was superficial and the white central, thus giving leaves that were green on the margin and a paler color in the center, on account of the white tissue in the center of the leaf. One of the plants grown from a green branch occurring on an albomarginate plant was of this nature. Its seed produced only ordinary green plants.

The origin of the mosaic seedlings from a cross between white margined and green is not yet fully clear. Careful study of such of these seedlings as were recorded pure white revealed indications of green tissue in the hypocotyls. Likewise, those regarded as pure green revealed indications of white tissue. All of the seedlings from the green-white cross are probably mosaics, the differences being due to the fact that in some of them the white tissue, in others the green, is confined to a few cells, the remainder of the plant developing from the other tissue.

It is important to note that in some of these mosaics, or marbled plants, white "islands" may appear in several parts of the plant. These islands are evidently not derived one from the other. It can, therefore, be asserted that the differentiation of these white cells occurs more than once during the development of a plant and that the white cells must result from the division of cells that are green in appearance. (It is important to remember that green is dominant in the cross.) Just when these white cells arise can not be stated so positively. They may certainly arise after the formation of the cotyledons has begun.

The author offers the following tentative explanation of the origin of this white tissue in the crossbred green-white plants. The fertilized ovum contains both green and white chromatophores. In cell divisions of the embryo the chromatophores are distributed to the daughter cells more or less according to chance. If a cell receives only white chromatophores this cell will have only white descendants. If a cell receives only green chromatophores its descendants will be pure green cells. A cell receiving both kinds may later produce either pure white or pure green at any cell division. Should a cell which is later to develop into cotyledons and growing point receive only one kind of chromatophores, then the resulting seedling will appear to be only pure white or pure green, as the case may be. Since pure white cells may have only pure white descendants and pure green only pure green, while mixed cells may have three kinds of descendants, it naturally follows that after many cell divisions the percentage of mixed cells in the plant practically vanishes.

The above hypothesis makes only one assumption that is not demonstrated; that is, that the fertilized egg cell has two kinds of chromatophores, namely: white and green. According to current teaching the chromatophores are derived entirely from the egg cell; but, according to the author, this may well be considered not an established fact. If current teaching on this point is correct, then we have here a very remarkable case. It would then be necessary, according to Dr. Baur, to assume that in the cross, female white on male green, a part of the white chromatophores of the egg may become green under the influence of the male nucleus, and that in the reciprocal cross a part of the white chromatophores would have to become green under the influence of the male nucleus. Such a condition is thinkable, but no such case is known. Should it be proven, however, that the male sexual cell carries chromatophores, then the inheritance of the albomarginate character is fully explained.

These results of Dr. Baur's call for a detailed study of the chromatophores from one sexual cell stage to the next. The writer would suggest another possible explanation of the phenomena discussed above. The male nucleus may bring with it into the cell something which is not a part of the nucleus itself but is cytoplasmic in its nature. This may develop and give rise to a part of the cytoplasm of the fertilized egg. Then something in the chemical constitution of this cytoplasm causes the chro-

matophores which develop in it to lose their power of assimilating $CO_2$. Subsequent cell division would occasionally throw off cells of pure white, which would give rise to the white tissue. This is only suggested as a mere possibility. That the condition can hardly be caused by the male nucleus itself would seem to be indicated by the fact that descendants of this nucleus must be present in those cells which are pure green. If the white character were carried by the chromosomes, then it would appear that all the green cells would necessarily be affected. There seems to be no question that the white character is cytoplasmic in its nature, and this would account for the fact that it does not follow Mendel's law of segregation in the reduction division. The segregation, in fact, occurs in somatic divisions.

Professor Correns reports another interesting study of variegation in a recent article,[3] of which the following is a summary.

Plants deficient in chlorophyll have hitherto been called "aureas." The author now restricts this term to plants which are deficient in chlorophyll but which have the normal amount of yellow-color materials, zanthophyll and carotin. Those deficient in all three are termed "chlorinas." Those of the latter type obtained in commerce were found to be dwarf as compared with normal sorts. The leaves and flowers are also relatively smaller. This smaller size is shown to be partly a consequence of deficiency in chlorophyll and the consequent insufficient nourishment of the plant. On the other hand, it is partly due to a specific Mendelian character of dwarfness, and the Mendelian dwarf habit is strictly correlated with small leaves and small flowers.

The chlorina races are fully constant. Variegated races have spots of green on leaves otherwise of chlorina type. In some cases these spots vary in number and size from leaf to leaf; in others they are hereditarily fixed. Some of the variegated races, on account of the smallness of the green spots, are difficult to distinguish from the chlorina types. On some of the variegated plants, especially those having much green, typical green branches occur, and this phenomenon is characteristic of the plants on which it occurs. That is, the same plant year after year produces these green branches. Every possible gradation

[3] Investigations on Inheritance of Yellowish Green and Variegated Races of *Mirabilis Jalapa*, *Urtica pilulifera* and *Lunaria annua*. *Zeitsch. f. Abst.- u. Vererb.*, 1, 1909, H. 4.

exists between a small green fleck on a leaf and a typical green branch.

The variegated types do not reproduce strictly true to seed. They sometimes throw green plants. These green plants do not simply represent extremes of variation because they are too numerous and offer a secondary maximum in the curve of distribution. On the other hand, variegated plants have thus far not produced any of the pure chlorina type. Some of the pure green reversions produced progeny all of which are green. A larger number gave some variegated and some green, the green nearly always predominating in the progeny. The thus obtained variegated plants gave some normal green progeny, and the normal greens thus obtained gave only occasionally all normal greens. A green branch on a variegated plant, when self fertilized, gave three variegated and four green plants. It was not possible to explain variegation in these species as a cross between the chlorina and the normal green types. In the cross between chlorina and typica (normal greens) the latter is dominant, but not absolutely so. The chlorophyll content of the hybrids is about 90 per cent. of that in the normal greens. In some cases in the second generation of this cross, the hybrids split into chlorinas and greens in perfect Mendelian fashion. In others variegated plants occur in the second generation; the reason for this is given below.

Dwarf and normal stature behave as a pair of Mendelian characters independent of leaf color, the dwarf habit being recessive. Generally speaking, chlorina plants not dwarf were not quite so tall as the normal greens because of their inability to manufacture starch at normal rate. The tall chlorinas and the dwarf greens produced from this cross were new types, the latter being especially attractive.

In the cross variegata on typica the latter is dominant and segregation occurred in Mendelian fashion. On account of the variability of the variegated type (this type produced some greens) the per cent. of greens in $F_2$ was somewhat in excess of 75 per cent. Here again the semi-dwarf and normal stature acted as a pair. In the cross between chlorina and variegata the latter proved to be dominant. Normal splitting occurred in the second generation. As in other cases, a few greens arose from the variegated plants. The medium stature of the variegated plants behaved as a pair with the dwarf stature of the chlorina plants.

In each of three experiments the cross variegata on typica gave chlorinas, variegated plants and normal greens in the ratio 1:3:12. The plants used in these crosses were known to be constant. In one experiment a cross between typica and chlorina gave in $F_2$ 63 green, 4 variegated and 3 chlorinas. Here also the chlorina form was known to be constant. This unusual behavior is explained by Professor Correns in the following manner:

The occurrence of normal greens amongst the progeny of variegata is due to the revival of a latent factor for green (G). The color factors present in the various types are assumed to be

G = presence; g = absence (or latency) of green factor.
V = presence; v = absence (or latency) of variegata factor.
C = presence; c = absence (or latency) of chlorina factor.
V is epistatic to C.
G is epistatic to V and C.
Variegated races have the formula gVC (or gVc).
Chlorina races have the formula gvC.
Normal green races have the formula GVC (or GvC, or GVc, or Gvc).

The cross between green and variegata thus becomes:

GVC + gVC, in which $F_2$ = 3 green to 1 variegated; or
GvC + gvC, in which $F_2$ = 12 green, 3 V and 1 C.

The cross green on chlorina becomes:

GvC + gvC, in which $F_2$ = 3 green to 1 chlorina; or
GVC + gvC, in which $F_2$ = 12 green, 3 V and 1 C.

The cross variegated on chlorina becomes:

gVC + gvC, in which $F_2$ = 3 V + 1 C.

The cross between the very distinct species *Mirabilis Jalapa variegata* and *M. longifolia* typica give hybrids that are quite alike in $F_1$, but highly variable in $F_2$. Yet all the characters involved appear to "Mendelize." For instance: green and variegated leaves, normal and dwarf stature, erect and trailing habit form Mendelian characters.

In contradistinction to the white margined *P. zonale* studied by Baur, a white margined form of *Lunaria annua* studied by Professor Correns reproduced true to seed, and when crossed with a green leafed form the margin behaved as a recessive Mendelian character.

A recent article by Whitney in the *Journal of Experimental Zoology*[4] is of interest in connection with the type of heredity

found by Baur in *P. zonale*, as it bears upon the relation of plastids in the cytoplasm to heredity. Eggs of *Hydatina senta* were subjected to centrifugal force, which separated the contents into three layers, described as a pink zone, a middle clear zone and a gray zone. The first cleavage plane was variously arranged with reference to these zones in different eggs, yet the eggs developed into normal adults which produced normal young. This would seem to indicate that the plastids in the pink and the gray zones have little to do with differentiation in development. This does not prove, however, that other plastids might not have such influence.

Professor Vernon L. Kellogg, of Leland Stanford University, has recently published an important paper on inheritance in silk worms.[5] In common with Coutagne and Toyama he found many Mendelian characters in these insects. This was especially the case for characters of the larvæ. For instance, the mouricaud pattern (a dark form) in the larvæ was dominant to white. The same was true of the tiger banded, or zebra, type of coloring. A white type with a well marked darker pattern, which in the laboratory is known as "the patterned type" behaved usually as a unit character recessive to zebra and dominant to white. Its behavior was entirely Mendelian in crosses with white, but there was some irregularity in crosses with zebra. The irregularities mentioned by Professor Kellogg are fully explained by assuming that the pattern character and the zebra character are independent Mendelian characters, and that when both are present in the same individual they can both be discerned.

The author was puzzled a good deal by the behavior of white and attributes the fact that it was sometimes dominant and sometimes recessive to individual or strain idiosynerasies. A large number of matings are given with their results in the first and second generation to illustrate the idiosyncrasies relating to inheritance of white. Evidently, Professor Kellogg was dealing with animals in which there are two distinct types of white, one dominant and the other recessive. A similar case has been well made out for poultry, and I have found indications of two such white characters in swine, though the recessive white in swine is not fully made out. All of the irregularities in the inheritance

[4] D. D. Whitney. Effect of a Centrifugal Force upon Development and Sex. *Journ. of Exp. Zool.*, VI, No. 1, January, 1909.

[5] Leland Stanford University Publications, University Series No. 1.

of white found by Professor Kellogg fall immediately into line with Mendelian principles by the assumption of these two types of white, which are sometimes found in the same individual.

Some of the most interesting work reported by Kellogg relates to cocoon coloring. He found one type of salmon colored cocoon which when crossed with either the dominant or the recessive white behaved as a Mendelian unit and broke up into every shade from very pale salmon to golden yellow. This is an interesting case of a variable Mendelian character. Generally speaking, the various cocoon colors were Mendelian units, the only irregularity being the marked variation of some of the colors after hybridization. Wing pattern in the adults and the color and adhesiveness of the eggs showed no Mendelian differences. Apparently the variations which occur in these characters are due to the fluctuations of a single Mendelian character, and hence no pairs are formed.

The effect of insufficient nutrition on the dominance of characters was studied, the results being entirely negative. Kellogg attributes the Mendelian nature of the larval color characters to their origin by mutation, while the fluctuating variability of cocoon characters are supposed to be due to their origin by selection of fluctuating characters. As pointed out by the writer elsewhere, the manner of origin of a character, whether by gradual modification or by sudden change, has no relation to its Mendelian behavior, so that the fact that certain characters behave as Mendelian characters is in no way an indication that they are mutations.

Certain characters which fluctuated widely, and in which no indication of Mendelian inheritance was found, were amount and quality of silk in the cocoon, wing pattern, wing venation, certain larval markings, degree of adhesiveness in eggs and the number of broods produced in a season. These characters present very interesting objects of study, and it is gratifying to learn that Professor Kellogg is giving them further attention. Coutagne is quoted to the effect that selection for ten years had no effect on the richness of silk. This is important in its relation to the effect of selection on fluctuating characters.

One of the races on which these studies were made lays eggs which are non-adhesive. When crossed with races laying adhesive eggs, the non-adhesiveness disappears and does not reappear even in the second generation ordinarily. This suggests

that non-adhesiveness is due to the latency of a character which is revived under the stimulus of hybridization. It is stated that wing pattern does not seem to be capable of any considerable modification by even a most careful and persistent selection. This is in line with all recent work on selection in fluctuating characters when the effect of hybridization has been eliminated.

Variations of wing venation are of special interest. They seldom took the form of additions to the system of veins, and when they did the modifications were only slight. Generally, these variations consisted of the loss of veins in part or in whole. In many cases veins became reduced to tracheæ without chitinous covering. In a few cases tracheæ appeared in what may be supposed to be the position of ancient veins, thus representing partial restorations of lost characters. Many sports occurred in wing pattern. Generally speaking, these were not hereditary. Melanism occurring as a sport showed a slight tendency to be inherited, and further studies of this matter are in progress. Occasional moths with power of flight and less frequently appearing individuals with rudimentary wings showed no tendency to transmit these characters.

Some of the most interesting features of Professor Kellogg's work are the marked fluctuations of characters whose stages can not be fixed by selection. Yet the fact that certain of the races were constant with respect to a particular stage of such a character, as, for instance, the Italian salmon with reference to cocoon color, which on hybridization breaks up and becomes highly fluctuating, is of great interest. The question whether fluctuations can be fixed by selections is as yet debatable. The Italian salmon seems to be such a fixed stage. On the other hand, some of Professor Kellogg's results indicate that the Italian salmon may be a compound character, a fact which might account for its variability. Perhaps long continued selection might, after a while, fix such characters, especially when the fluctuations cover such a wide range. The writer hardly agrees with the assumption that such characters are non-Mendelian. It would seem rather that their stages are simply not stable from generation to generation. If they could be fixed by selection or otherwise one might then expect the fixed stages to behave toward each other as Mendelian pairs.

Dr. East reports some interesting studies on inheritance in

sweet corn.[6] He points out that Correns has shown that the peculiarity of sweet corn is due simply to inability to complete the formation of normal maize starch. The presence and absence of this starch forming ability behaves as an ordinary Mendelian pair. The absence of the ability to form starch is the one character peculiar to the sweet corn group. It is shown that the sweet corn may be either of the dent or the flint type in potential hereditary characters, and suggests that the early history of sweet corn indicates that it arose amongst the flints and spread to the dents by hybridization. Dent corns tend to have from 12 to 28 rows; flints usually have 8 and may have 12 rows as the mode. Dents are little given to tillering, while tillering is characteristic of flints. Flint varieties are also characterized by large bracts at the end of the husks, dents by small bracts or none. Sweet corn, on the other hand, runs the whole gamut of the above characters. For instance, Stowell's Evergreen is a dent, having 16 to 24 rows. Golden Bantam and Black Mexican are flints.

When the starch forming character is introduced into sweet varieties from either dent or flint sources the dent or flint character of the sweet parent becomes evident. The author thinks that the dent or flint character appearing in sweet corn is determined largely, but possibly not entirely, by the character possessed by the female parent.

W. J. SPILLMAN.

[6] E. M. East. A Note Concerning Inheritance of Sweet Corn. *Science*, N. S., XXIX, No. 742.